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CHELID TURTLES (PLEURODIRA, CHELIDAE) FROM THE MIOCENE CAMFIELD BEDS, NORTHERN TERRITORY OF AUSTRALIA, WITH A DESCRIPTION OF A NEW GENUS AND SPECIES

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ABSTRACT

The Bullock Creek Local Fauna (mid Miocene Camfield Beds, Northern Territory of Australia) contains five or possibly six species of chelid turtles (Pleurodira: Chelidae), though only one form is sufficiently represented to be named. *Birlimarr gaffneyi* gen. et sp. nov. is a small (carapace length: 160 mm), short-necked species represented by a complete skeleton. A phylogenetic analysis of cranial and shell characters resolves the new genus as quite derived amongst Australian short-necked chelids, the plesiomorphic sister taxon to a clade composed of *Emydura* plus an *Elseya dentata* 'generic group'. Three other forms are diagnosed on shell material to genus or suprageneric level: a large (carapace length ca. 440 mm) short-necked form is designated gen. aff. *Emydura/Elseya* sp. indet. and two long-necked forms are designated *Chelodina* sp. A and sp. B. Additional shell material indicates a fifth and possibly a sixth chelid species is present in the assemblage, but the lower level affinities of these forms cannot be determined. The *Emydura/Elseya* form is similar but not identical to previously described '*Emydura*' material from the Miocene of South Australia (Wipajiri and Namba Formations), while a previously described carapace from the Miocene of western Queensland (Carl Creek Limestone) may represent a species of *Birlimarr* gen. nov. The Carl Creek Limestone and Camfield Beds assemblages are similarly diverse, approximating the maximum sympatric diversity recorded in extant assemblages: palaeoenvironmental conditions at these two Miocene localities thus appear to have been optimal for chelid diversity. Many of the Camfield Beds specimens show evidence of predation by crocodiles.

KEYWORDS: Chelidae, Pleurodira, *Birlimarr gaffneyi*, new genus, new species, Miocene, Camfield Beds, Northern Territory, Australia, phylogeny, phylogenetic analysis, palaeoecology.

INTRODUCTION

The Chelidae is a family of pleurodirous ('side-necked') freshwater turtles whose living representatives are today found in South America, Australia and New Guinea (plus some eastern Indonesian islands - Rhodin 1994). The Australasian and South American representatives are generically distinct (Fig. 1). Chelid turtles are relatively common in the Cainozoic vertebrate fossil assemblages of Australia, and the better material has been described or reviewed in Warren (1969), Gaffney (1979a; 1981, 1991), Gaffney *et al.* (1989), Burke *et al.* (1983), White and Archer (1994), White (1997) and Thomson *et al.* (1997).

Chelid turtles comprise a significant component of the Miocene Bullock Creek Local Fauna (LF) from the Camfield Beds of northern Australia (Murray and Megirian 1992), but have not previously been analysed. Most of the material assembled by the Museums and Art Galleries of the Northern Territory (NTM) consists of disassociated carapace and plastron fragments representing numerous individuals, with only a few other post-cranials and even fewer disarticulated cranial bones, though additional isolated cranial and post-cranial bones are expected to be found when the finer residues of acid preparation are more thoroughly sorted. Such representation, together with a very limited

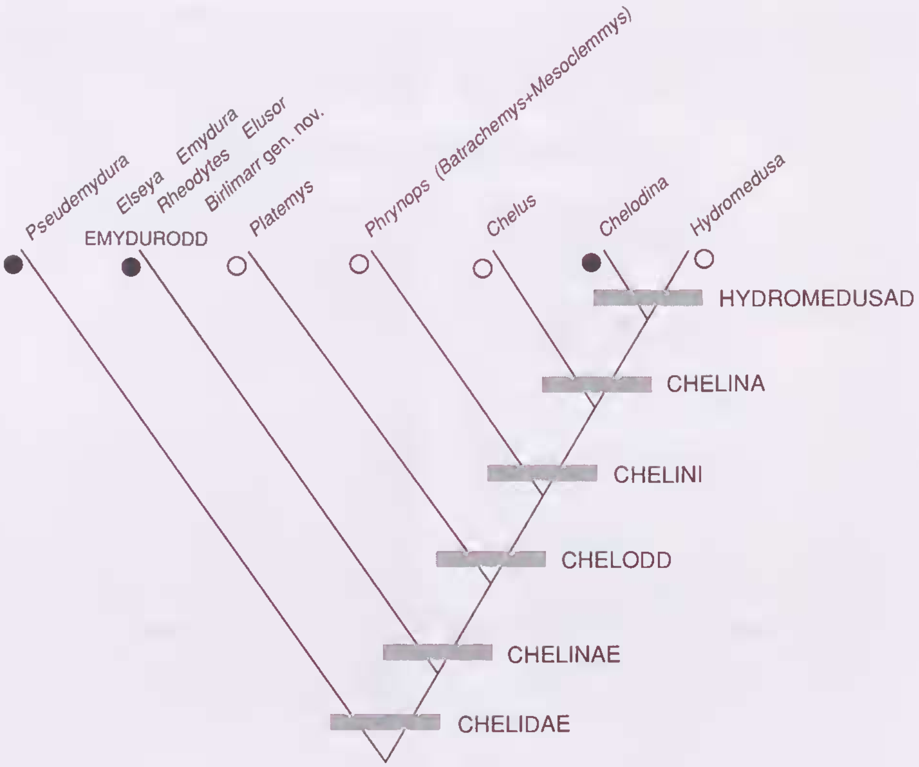


Fig. 1. Theory of relationships within the Chelidae based on shared, derived cranial characters, with the systematic nomenclature of Gaffney (1977). Solid circles indicate Australasian genera, open circles indicate South American genera. (after Gaffney 1977: fig. 10).

literature on the comparative osteology of extant Australian chelid species, inspired no attempt to interpret the affinities of the assemblage until a complete skeleton, the holotype of *Birlimarr gaffneyi* gen. et sp. nov., was collected in 1992 (Fig. 2).

The main objectives of this paper are to describe the Bullock Creek LF chelid fossils, to evaluate how many species may be represented, to investigate what the possible relationships of these may be to extant taxa and previously described Miocene forms, and to comment on the palaeoecological significance of the assemblage.

Only one morphotype, *Birlimarr gaffneyi* gen. et sp. nov., is sufficiently represented at this time to be assigned a binomial. Three other forms, however, can be diagnosed to a genus or suprageneric group on the basis of a selected reference specimen: gen aff. *Elseya/Emydura* sp. indet., *Chelodina* sp. A and *Chelodina* sp. B.

Various additional 'forms' are recognised in the comparative study of individual bones. Within that section, specimens which cannot be referred to the diagnosed taxa are designated 'forms' of some recognised group of chelids, i.e. at whatever taxonomic level can be resolved. These form designations apply only within the set of a particular bone - it should not be understood that, for example, epiplastron 'form 1' represents the same species as entoplastron 'form 1': no hypothetical taxa are proposed on the basis of observations as to which isolated bones seem to conform best to other isolated bones. The comparative analysis is aimed at determining the minimum number of morphospecies and individuals that accounts for the NTM Bullock Creek LF

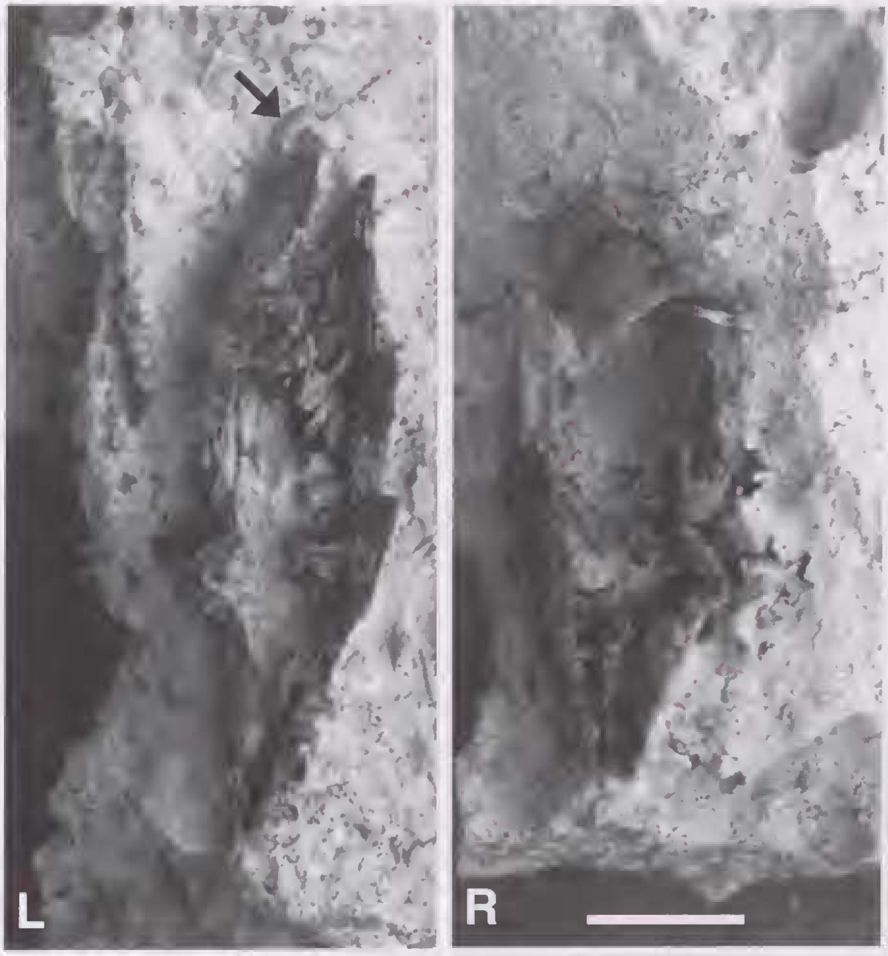


Fig. 2. *Birlimarr gaffneyi* gen. et sp. nov. holotype P9215-1, left and right halves partially acid etched out of Camfield Beds calcimudstone. Anterior towards the top, skull arrowed. Scale bar: 20 mm.

chelid assemblage as a whole, to investigate the diagnostic potential of certain bones, and to contribute to the comparative osteology of living and extinct Australian chelids.

Materials and methods. The described fossils were extracted from their limestone matrix using dilute (≈10%) acetic acid. All NTM Bullock Creek Local Fauna chelid bones that could be identified as such were examined as part of this study, but only specimens which were found to be informative in terms of the stated objectives are reported here. Representatives of each bone were compared with each other, and sorted into apparently natural groups on the basis of their morphological similarities, using the listed comparative material of extant species and cited literature on chelids as a guide. The contents of each set of bones were examined to see whether fragmented bones could be united into more complete specimens. Next, the contents of each set of carapacial and plastral bones that are in sutural contact in the chelid skeleton were compared in turn with each other, in order to identify more complete individuals wherever possible.

Terminology for the bones of the shell and epidermal scutes follows Zangerl (1969), and cranial anatomy follows Gaffney

(1979b). The combined axillary and inguinal buttresses of the shell are referred to as the bridge. The paired bones and scutes of the turtle shell are not always equal in length at their medial contacts. Where paired structures are referred to, interlaminal measurements, that is the average of left and right sides along their medial contact, should be assumed unless otherwise indicated.

Introductory remarks on chelid systematics and taxonomy. The current classification of Australian chelid species is poorly founded, relying substantially on differential diagnosis rather than on well-tested phylogenetic hypotheses. Manning and Kofron (1996) review and comment on the development and current state of Australian chelid systematics, and the reader is referred to their work for a more comprehensive overview: the histories of various ideas discussed herein are not traced from their origins.

In current classification of Australian chelids (e.g. Cogger 1996), there are five nominal genera of short-necked turtles: *Emydura, Elseya, Elusor, Rheodytes* and *Pseudemydura*, the last three of which are monospecific. 'Long-necked' turtles are all included in *Chelodina*. Georges and Adams (1992) proposed a phylogeny of Australian chelids based on allozyme electrophoresis. That phylogeny, reproduced here as Figure 3, indicates basic generic-level natural groups by which this and other phylogenetic hypotheses can be tested using morphological character states. We follow Thomson *et al.* (1997) in referring to the species (some still undescribed) clustering with *Elseya dentata* and those clustering with *Elseya latisternum* as the *Elseya dentata* and *Elseya latisternum* 'generic groups', that is, generic level clades requiring diagnosis and formal taxonomic revision. On the other hand 'species complexes' are apparently related species that are not sufficiently distinctive to warrant generic level distinction.

Gaffney (1977) presented a generic level cladistic phylogeny of the Chelidae relying primarily on skull characters; his preferred hypothesis and systematic arrangement here reproduced as Figure 1. Gaffney (1977) was obliged to treat *Emydura* and *Elseya* as congeneric because of inadequate documentation of the cranial osteology of the two nominal genera, and also because of the limited amount of objectively identified comparative skeletal material at his disposal. The comparative osteology of Australian chelids remains very incomplete. Legler and Cann's (1980) description of *Rheodytes leukops* and Cann and Legler's (1994) description of *Elusor macrurus* are also useful sources of information on *Emydura* and *Elseya*. The term '*Emydura/Elseya*' is applied here to fossil material where a soundly-based assignment to *Emydura* or one of the two *Elseya* generic groups is not possible. Our '*Emydura/Elseya*' is therefore essentially equivalent to Gaffney's '*Emydura*'.

Higher level systematics follows Gaffney (1977) and Gaffney and Meylan (1988), but attention is drawn to recent work by Georges *et al.* (in press) based in mitochondrial and nuclear gene sequence variation, which leads to some significantly different conclusions about chelid phylogeny (Fig. 4). Taxonomic changes proposed by Georges *et al.* (in press) on the basis of their work are not introduced here. As this study is not concerned with the higher level systematics and taxonomy of the group, nor with the relative merits of biochemical and morphological approaches to phylogeny reconstruction, the selected phylogenies of Georges *et al.* presented here as Figure 4 are simply treated as hypotheses to be tested, insofar as they depict possible relationships amongst chelids.

Gaffney (1977) erected the infrafamily Emydurodd to accommodate the short-necked genera *Emydura* and *Elseya*, observing that placing a species in *Emydura* (or *Elseya*) is akin to stating that it is structurally primitive for a chelid: Emydurodd is a taxon for which no shared, derived morphological character states have been identified. Both *Elusor* and *Rheodytes* are diagnosed by autapomorphies of their type and only species: thus *Rheodytes* was added to Emydurodd by Gaffney *et* al. (1989), and *Elusor macrurus* Cann and Legler, 1994, is clearly also a member. Emydurodd thus comprises all short-necked chelids except *Pseudemydura*. The concept of Emydurodd as a natural group within the Chelidae is supported by the work of Georges and Adams (1992, 1996) and Georges *et al.* (in press) (Figs 3 and 4).

Institutional abbreviations. AM - Australian Museum, Sydney; AMNH - American Museum of Natural History, New York; SMF - Senckenberg Museum, Frankfurt; MUZ - Monash University, Department of Zoology, Victoria; NMV - Museum of Victoria; NTM - Museums and Art Galleries of the Northern Territory (Northern Territory Museum); QM - Queensland Museum; UCMP - University of California Museum of Paleontology; UTG - University of Tasmania, Department of Geology; UU - University of Utah; WAM - Western Australian Museum.

Where no institutional prefix is given, it can be taken that the specimen is from the NTM collection.

Anatomical abbreviations.

Cranium

ang	angular
art	articular
bo	basioccipital
bs	basisphenoid
den	dentary
fr	frontal
ju	jugal
mx	maxilla
na	nasal
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qu	quadrate
so	suproccipital
sq	squamosal
vo	vomer

Shell

BCS	bridge carapace suture
C_{1-5}	costal bones
m_{1-12}	marginal scutes
P_{1-11}	peripheral bones
p_{1-4}	pleural scutes
v_{1-5}	vertebral scutes

Comparative material. *Chelodina longicollis* R.24812, det. S. Thompson, labelled 'UK004', no other data; *Chelodina rugosa* R.24815, Darwin area, Northern Territory, coll. L. Taylor, July 1986; R.24813, ex Parks and Wildlife Commission of the Northern Territory, Darwin area, no other data; R.24814, coll I. Archibald, Humpty Doo, Northern Territory, 1 February 1996; *Chelodina novaeguineae* R.16325, Kalala Station, Northern Territory, coll. R. Kennett, 29 April 1990; *Emydura macquarrii*, R.24816 female, R.24817 male, donated G. Fyfe, ex pet-shop trade from Murray River, South Australia, no other data; *Elseya dentata* R.24818, male, Katherine River, Northern Territory, 14° 21'S, 132° 25'E, coll. I. Archibald, 14 September 1998; *Emydura victoriae* R.24819, Longreach Billabong, Elliott, Northern Territory, coll. G. Fyfe, (species thought to have been introduced to this waterway in historical times); *Emydura* sp. R.24820, sub-adult, no other data.

SYSTEMATICS

Testudines Linnaeus
Pleurodira Cope
Chelidae Gray
Chelinae Gray
Emydurodd Gaffney, 1977
***Birlimarr* gen. nov.**

Type species. *Birlimarr gaffneyi* sp. nov.

Diagnosis. As for *Birlimarr gaffneyi* sp. nov.

Etymology. *Birlimarr* - turtle in the language of the Mudburra Aboriginal people of the Camfield district (*Tjambutjambulani*), Northern Territory (David Nash pers. comm.; Tindale 1974).

Birlimarr gaffneyi sp. nov.

(Figs 2, 5-8, 10-12; Tables 1-3)

Type material. HOLOTYPE NTM P9215-1, virtually complete skeleton.

Type locality, stratigraphy, fauna and age. Calcimudstone facies of the Camfield Beds; 'Top Site' of the Bullock Creek Local

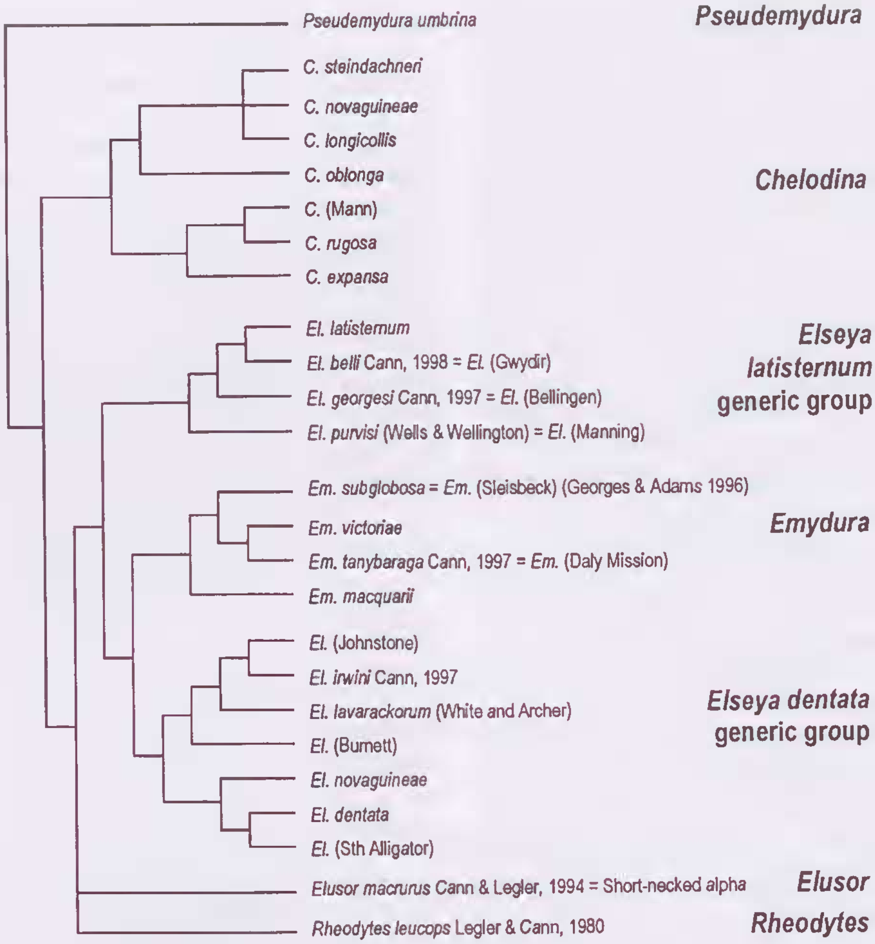

Pseudemydura umbrina
Pseudemydura
C. steindachneri
C. novaguineae
C. longicollis
C. oblonga
Chelodina
C. (Mann)
C. rugosa
C. expansa
El. latisternum
El. belli Cann, 1998 = El. (Gwydir)
El. georgesi Cann, 1997 = El. (Bellingen)
El. purvisi (Wells & Wellington) = El. (Manning)
Elseya latisternum generic group
Em. subglobosa = Em. (Sleisbeck) (Georges & Adams 1996)
Em. victoriae
Em. tanybaraga Cann, 1997 = Em. (Daly Mission)
Em. macquarii
Emydura
El. (Johnstone)
El. irwini Cann, 1997
El. lavarackorum (White and Archer)
El. (Burnett)
El. novaguineae
El. dentata
El. (Sth Alligator)
Elseya dentata generic group
Elusor macrurus Cann & Legler, 1994 = Short-necked alpha
Elusor
Rheodytes leucops Legler & Cann, 1980
Rheodytes

Fig. 3. Phylogenetic hypothesis of Australian freshwater turtles after Georges and Adams (1992: fig. 6), based on allozyme biochemistry of short-necked species excluding *Pseudemydura* (i.e. Emydurodd of Gaffney 1977). *Pseudemydura* and *Chelodina* were not analysed biochemically in that study, but added in on other grounds. New species names added, with an allozyme based phylogeny within the *Elseya dentata* generic group supplied by S. Thomson (written comm.): see also Georges and Adams (1996). Basic generic level taxa recognised in this work added on the right. See Cann (1998) for discussion of *Elseya purvisi* Wells and Wellington, and Thomson *et al.* (1997) for *Elseya lavarackorum* (White and Archer).

Fauna, latitude 17° 07'S, longitude 131° 31'E; mid Miocene on the basis of marsupial stage-of-evolution biochronology. (Plane and Gatehouse 1968; Woodburne *et al.* 1985; Rich 1991; Murray and Megirian 1992; Megirian 1994a; Murray *et al.* in press).

Referred material. All listed sites (quarries) mentioned with referred material are in close proximity to the type locality (i.e. 'Top Site'). Material for which no site name was recorded (i.e. 'unrecorded quarry') is either from the type locality or one of the nearby sites (Murray and Megirian 1992: fig. 2). P9612-2 (Top Site), left epiplastron; P906-22 (Site X), left epiplastron; P9464-157 (Top Site), entoplastron; P9464-156 (Top Site), posterior portion of entoplastron; P9464-149 (Top Site), left hyoplastron; P944-10

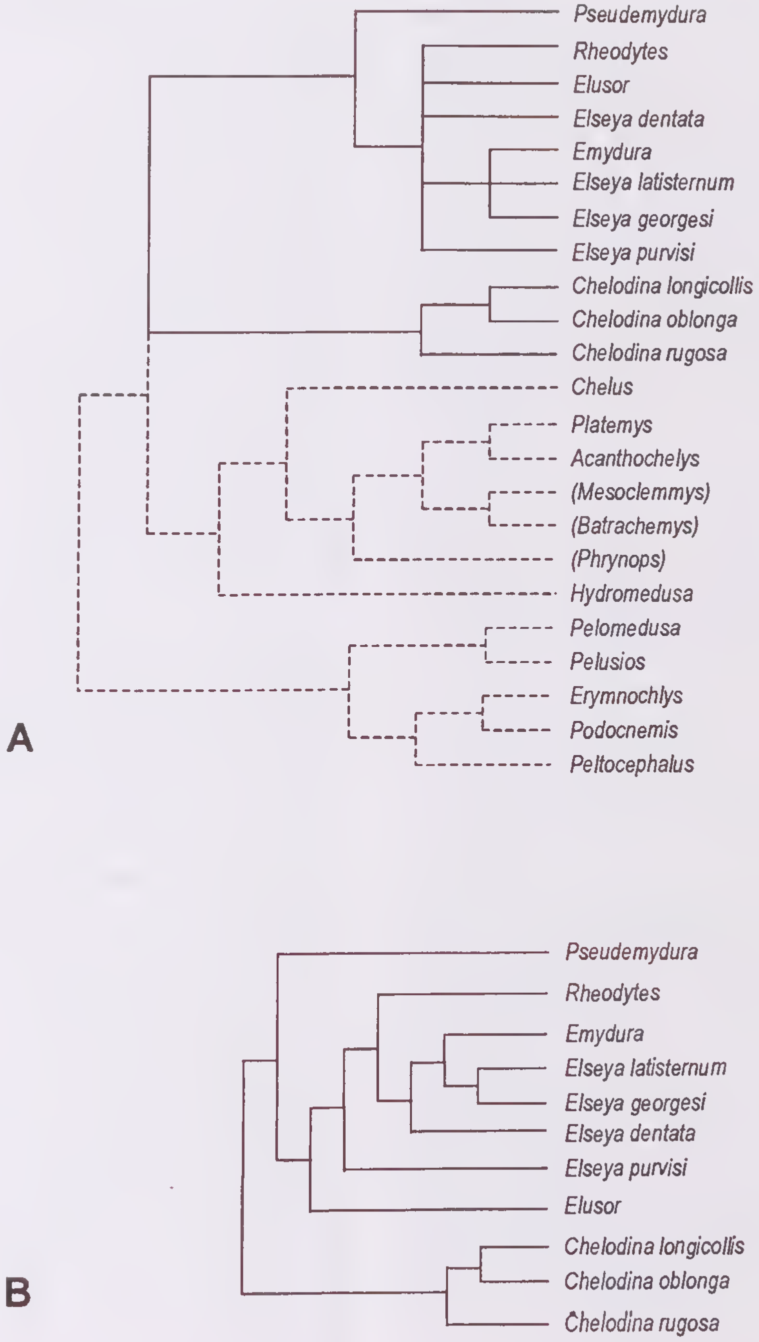


Fig. 4. Phylogenies **A**, of living pleurodires (Australasian taxa connected by solid lines, South American and African taxa connected by dashed lines) and **B**, of Australian chelids, generated from partial sequences of mitochondrial and nuclear genes, after Georges *et al.* (in press: figs 3, 4). Taxa shown in brackets are subgenera of *Phrynops*.

(unrecorded quarry), right hyoplastron; P9464-166 (Top Site), right hypoplastron; P925-5 (Site Y), right hypoplastron; P9464-126 (Top Site), right xiphiplastron; P87105-17 (unrecorded quarry), right costal 1; P9464-137 (Top Site), right costal 1; P9464-138 (Top Site), right costal 1; P9464-139 (Top Site), right costal 1; P9464-140 (Top Site), right costal 1; P9464-142 (Top Site), right costal 1; P9276-6 (Top Site), left costal 1; P9464-135 (Top Site), nuchal; P9464-148 (Top Site), nuchal; P87113-50 (Site Y), right costal 8; P87103-53 (Blast Site), left costal 8.

Diagnosis. Small species of Emydurodd, adult straight line carapace length *ca.* 160 mm. Carapace regularly oval in dorsal view, evenly and quite strongly domed in transverse profile, no indication of axial ridge or depression. Cervical scute present. Vertebral scutes all wider than long. Vertebrals 1 and 5 similar in width, but distinctly narrower than three intervening scutes. Interpleural seams contact marginal scutes 5, 7 and 9. Plastron, excluding bridges, half maximum width of carapace, length 90% of carapace; carapace and plastron with equal anterior projection, carapace overhanging plastron posteriorly. Anterior and posterior lobes of plastron arc gently upwards. In ventral view, margin of the anterior plastral lobe tapers gently forward of the bridge, with blunt, slightly squared-off anterior margin. Femoral scute area of posterior lobe bulges laterally; posterior extremity as covered by anal scutes comparatively small. Intergular about half as wide as long, marginal, completely separating gulars, partially separating humerals. Cranium proportionally low, broad and short, orbits large such that orbital diameter is about 25% of basicondylar length. Supraoccipital spine short, projecting posteriorly to about same extent as occipital condyle. No medial triturating ridge on maxilla. Ventral flanges of frontals vertical and parallel. Pterygoid-palatine suture almost straight, oriented at 45° to axial plane. Pterygoid-quadrate suture long in ventral view, oriented anterolateral to axial plane. Mandible gracile, dentaries fused.

Description. *Taphonomy and stratinomy of the holotype.* The preservation of P9215-1 is unusual for Camfield Beds vertebrates in particular, and for Australian Cainozoic deposits in general, and consequently is described in some detail.

The holotype was found embedded in facing walls of a naturally fractured calcimudstone boulder. Fracturing bisected the skeleton near the axial plane. The shell was crushed dorsoventrally, but not isometrically. On the plane of the fracture, crushing was greatest near the mid and anterior regions, relatively less posteriorly. Partial preparation revealed that some appendicular bones were also broken, and that few bones were in true articulation, but were closely associated with their near anatomical neighbours (Fig. 2).

Removal of limestone matrix by acid etching results in the loss of support of individual bones. Spatial relationships between bones are thus difficult to preserve or record fully with this kind of preparation. On the other hand, acid etching produces undamaged tiny bones, as well as excellent surface-detail, both easily lost in mechanical preparation, especially where the matrix is harder than the fossil. To optimise the taphonomic information that could be recovered during preparation, it was decided to partially restore the shell as it was extracted, and to periodically collect other post-cranials from where they settled, keeping associated pieces together as much as possible. This was achieved by orienting the specimen in the acid tub so that released elements settled more or less *in situ*, rather than in the bottom of the tub. In practice, this method worked for the larger bones, but phalanges, for example, were very difficult to recognise amongst all the other insolubles released. After hand-picking the larger bones, remaining insolubles were screened down to 0.5 mm, and additional bones recovered when the yield was scanned under the microscope.

Re-assembly of the shell (Figs 5-6) resulted in a specimen that is closer to the morphology of the animal in life, rather than a true record of its former arrangement in the matrix, but it remains possible to account for many of the breaks and dislocations. These can be attributed to several mechanisms: the event or events causing anisometric crushing and disarticulation; post-depositional rearrangement of bones; post-lithification fracture of the host limestone and subsequent weathering; and accidental breakages that occurred during collection and acid preparation.

Wherever possible, accidental breakages, which comprise only a small proportion of the damage visible in the specimen, were repaired as soon as possible after they occurred. The two halves of the shell (plastron + carapace) match exactly at only a couple of points (Fig. 5): elsewhere, weathering resulted in the loss of up to 12 mm of bone. The remaining damage consisted of separations at sutures, many of which were realigned in restoration, and breakages attributable to crushing.

On the carapace, left pleurals 2 to 4 were broken transversely. Two indentations are visible on the break, one on the suture of the first and second pleural, and the other on the suture of the second and third pleural. A possible third indentation lies medial to the fracture on the fourth pleural. On the left plastron, more or less opposing the damage to the carapace just described, are complex fractures radiating from a depressed puncture at the epi-entoplastron suture.

The right carapace preserves another major fracture coursing obliquely from the midline at the third pleural to the margin of the third peripheral. The right plastron is broken in a comparable fashion to the right carapace. However, no punctures or indentations can be distinguished on or near the major fracture on the right side.

The damage on the left hand side is consistent with an attack by a crocodile, of which three species are known to occur in the Bullock Creek Local Fauna (*Baru darrowi* Willis *et al.* 1990; *Harpacochampsa camfieldensis* Megirian *et al.* 1991; and *Quinkana timara* Megirian 1994b). The three species have different dentitions, but the opposing tooth indentations and punctures on the turtle are insufficiently developed to establish which might have been responsible. Although no undoubted tooth punctures are associated with the fractures on the right hand side, they are probably related to the same event.

P9215-1 evidently died from a mortal wound inflicted by a crocodile. Severe crushing resulted in the fracturing of internal bones as well as the plastron and carapace, which also suffered separations at sutures. The turtle was perhaps then released for a second strike, but lost by its attacker. It settled in still water at the bottom of a pond or lake, where decomposition, scavenging and/or bioturbation by small animals resulted in minor dislocations of the remains. Rapid precipitation of the fringing calcite cement that is typically present on bioclasts in fossiliferous facies of the Camfield Beds, followed closely in this case by burial in microdetrital carbonate, ensured its preservation.

Shell (Figs 5-7). In dorsal view, the carpace is an almost regular oval, about one third longer (total length 162 mm) than its maximum width (121 mm) which occurs at about the level of peripheral 7. The carapace is quite strongly domed, with no trace of an axial crest or depression. The lateral edges from peripherals 1-6 are sharply upturned, but only very gently so elsewhere, and there are no marginal serrations posteriorly. Carapacial fenestrae are absent, the pleurals being strongly sutured to the peripherals, and therefore indicating an adult stage of development.

The plastron excluding the bridge is almost exactly half the maximum width of the carapace. The maximum length approaches 90% of that of the carapace. Anterior extent of the upper and lower parts of the shell is equal, the carapace overhanging the plastron posteriorly. In lateral view, the anterior and posterior lobes are gently upwards. In ventral aspect, the laterally edges of anterior lobe taper very gently forwards to the blunt, slightly squared-off anterior margin. The posterior lobe, on the other hand, bulges laterally behind the bridge, with the posterior extremity as covered by the anal scutes small and W-shaped.

The relationships of bones to epidermal scute areas are shown in Figure 5C-D. The vertebral scutes of the dorsal shield are all wider than they are long. Vertebrals 2, 3 and 4 are of about equal width, becoming shorter posteriorly. Vertebrals 1 and 5 are similar in width to each other but distinctly narrower

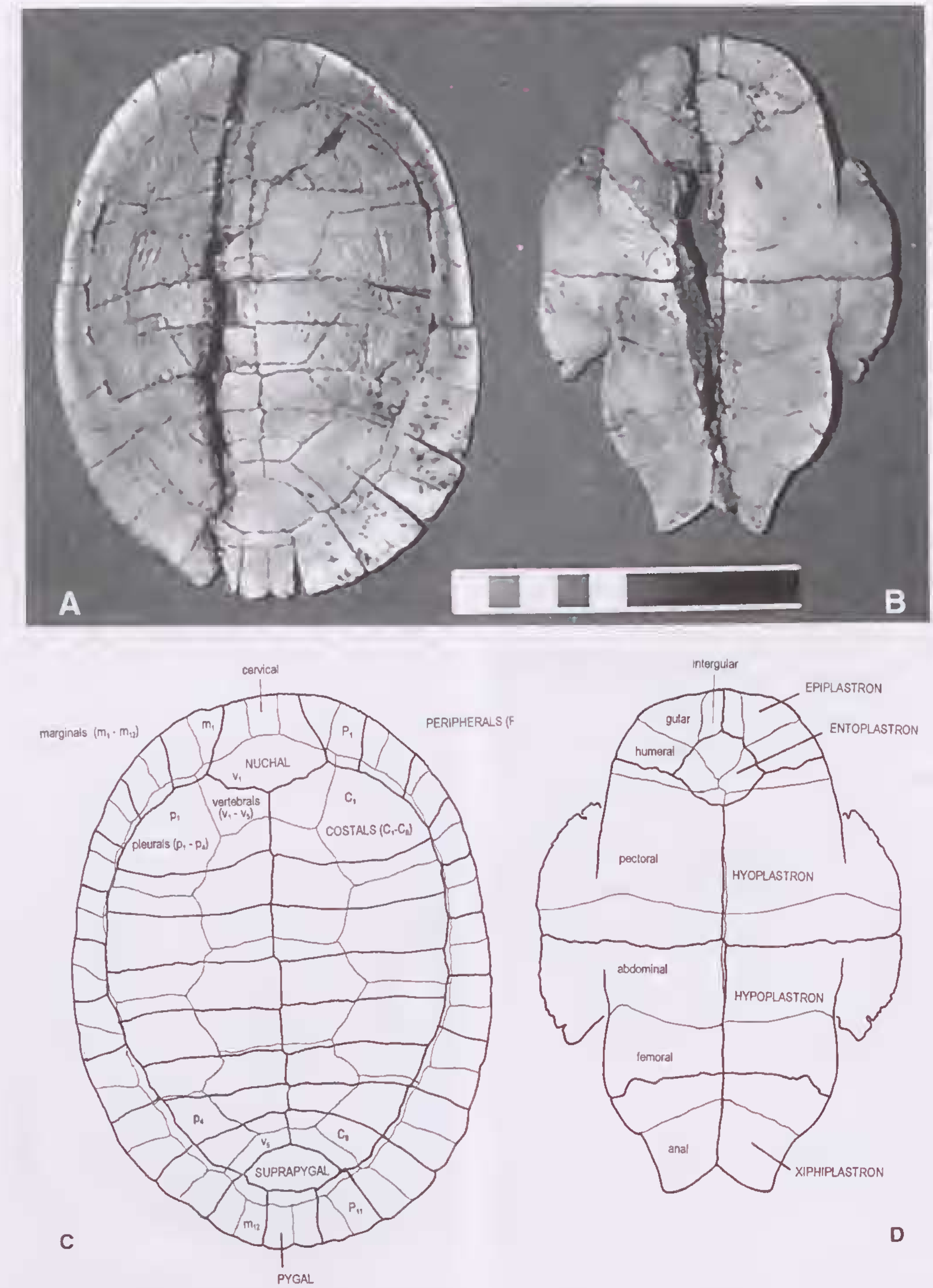


Fig. 5. *Birlimarr gaffneyi* gen. et sp. nov. holotype P9215-1. **A**, dorsal view of carapace and **B**, ventral view of plastron, with **C** and **D**, restored interpretive diagrams showing the relationships of bones to epidermal scute areas. Bones delimited by heavy lines and labelled in upper case, scutes delimited by fine lines and labelled in lower case.

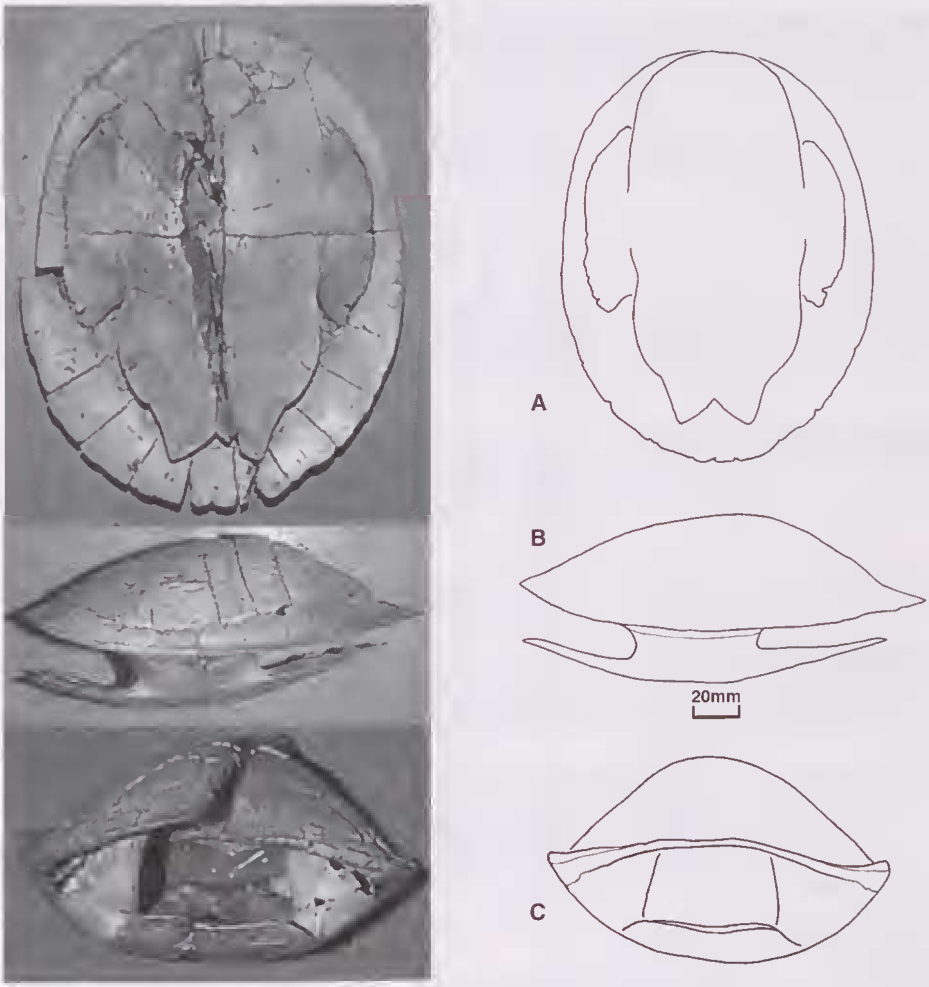


Fig. 6. *Birlimarr gaffneyi* gen. et sp. nov. holotype P9215-1 in: **A**, ventral; **B**, left lateral; and **C**, anterior views, with restored outlines showing the shape of the shell.

than the three intervening scutes. There is a relatively broad cervical scute on the nuchal bone. The interpleural seams contact marginal scutes 5, 7 and 9 (Table 1). The intergular of the ventral shield completely separates the gulars, but only incompletely separates the humerals, therefore not coming into contact with the pectorals. The intergular scute area is about half as wide as it is long. The modal plastral formula (Table 2), to the extent that preservation allows it to be determined, is pectoral > abdominal > intergular > femoral > anal.

The axillary buttress of the bridge is strongly sutured to the first costal by a broad, deep sutural contact (Fig. 7), which is widest medially, constricting only slightly anterolaterally. The trace of the suture diverges anterolaterally from the trace of the first rib.

Skull. In general terms, the skull of P9215-1 (Fig. 8) has the typical form of Australian short-necked chelids excluding *Pseudemydura*, and also shows some general similarities to the South American *Platemys platycephalus* (Fig. 9). The cranium is slightly flatter in lateral profile than the figured species of *Elseya* and *Emydura*, but not as flat as *P. platycephalus*. The degree of lateral cheek emargination is similar in all these taxa. The supraoccipital has small

Table 1. Comparison of osteological characters of Australian short-necked chelids, abstracted from: (Gaffney 1977: tables 2, 3); Legler and Cann (1980: table 1); Cann and Legler (1994: table 4); Thomson *et al.* (1997: table 1); and this work.

	Pseudemydura umbrina	*Emydura*	*Elseya dentata* (GG)	*Elseya latisternum* (GG)	*Rheodytes leucops*	*Elusor macrurus*	*Birlimarr gaffneyi* gen. et sp. nov.
Anterior process of frontal	absent	present	present	present	present	present	present
Size of postorbital	large	small	small	small	small	small	large
Temporal arch	extensive: formed by parietal, squamosal and supraoccipital	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal
Dorsal (horizontal) portion of parietal	broadly covers adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa
Lateral edges of parietals	sub-parallel but laterally extensive	sub-parallel	tapering anteriorly	tapering anteriorly	tapering anteriorly	tapering anteriorly	parallel
Supraoccipital-parietal contact	present	absent	absent	absent	absent	absent	absent
Quadrate-parietal contact	present	absent	absent	absent	absent	absent	absent
Dorsal (horizontal) portion of supraoccipital	broadly expanded	not expanded	not expanded	not expanded	elongate, but not expanded laterally	not expanded	not expanded
Crista supraoccipitalis	does not extend beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	does not extend beyond occipital condyle
Squamosal expanded anteriorly	yes	no	no	no	no	no	no
Medial maxillary contact dividing premaxillae longitudinally	yes	no	no	no	no	no	?
Mandibles	weak, without symphyseal hook	massive with symphyseal hook	massive with symphyseal hook	massive with symphyseal hook	weak, without symphyseal hook	massive with symphyseal hook	weak, weakly developed hook
Prearticular separates or nearly separates coronoid splenial	yes, when present	no	no	no	splenial absent	no	?

dorsal expression, projecting posteriorly only just as far as the occipital condyle. In this respect, P9215-1 is intermediate between *P. platycephalus*, in which the occipital condyle projects beyond the supraoccipital spine, and *Elseya* and *Emydura* in which the opposite is the case. P9215-1 is broad in relation to its length, compared to *Elseya, Emydura* and *Platemys*. The orbits are proportionally large, having a diameter of about 25% of the basicondylar length. Proportionally large orbits appear to be to some degree an allometric feature of small individuals and species, but not even in the smallest chelid specimens of other chelid species illustrated in Figure 9 does the ratio of orbit diameter to basicondylar length appear to be as high as it is in the fossil form.

The nasals are not represented in P9215-1, but it can be surmised from the continuous sutural surface around the anterior processes of the frontals that nasals were present and that the frontals did not form part of the dorsal anterior margin of the external narial aperture. Neither dorsal flange of the prefrontal is intact, but the nasal suture on

Table 1 cont. Comparison of osteological characters of Australian short-necked chelids, abstracted from: (Gaffney 1977: tables 2, 3); Legler and Cann (1980: table 1); Cann and Legler (1994: table 4); Thomson *et al.* (1997: table 1); and this work.

	Pseudemydura umbrina	*Emydura*	*Elseya dentata* (GG)	*Elseya latisternum* (GG)	*Rheodytes leucops*	*Elusor macrurus*	*Birlimarr gaffneyi* gen. et sp. nov.
Anterior process of frontal	absent	present	present	present	present	present	present
Size of postorbital	large	small	small	small	small	small	large
Temporal arch	extensive: formed by parietal, squamosal and supraoccipital	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal	moderate: formed by squamosal and parietal
Dorsal (horizontal) portion of parietal	broadly covers adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa	covers central, but not lateral, area of adductor fossa
Lateral edges of parietals	sub-parallel but laterally extensive	sub-parallel	tapering anteriorly	tapering anteriorly	tapering anteriorly	tapering anteriorly	parallel
Supraoccipital-parietal contact	present	absent	absent	absent	absent	absent	absent
Quadrate-parietal contact	present	absent	absent	absent	absent	absent	absent
Dorsal (horizontal) portion of supraoccipital	broadly expanded	not expanded	not expanded	not expanded	elongate, but not expanded laterally	not expanded	not expanded
Crista supraoccipitalis	does not extend beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	extends beyond occipital condyle	does not extend beyond occipital condyle
Squamosal expanded anteriorly	yes	no	no	no	no	no	no
Medial maxillary contact dividing premaxillae longitudinally	yes	no	no	no	no	no	?
Mandibles	weak, without symphyseal hook	massive with symphyseal hook	massive with symphyseal hook	massive with symphyseal hook	weak, without symphyseal hook	massive with symphyseal hook	weak, weakly developed hook
Prearticular separates or nearly separates coronoid splenial	yes, when present	no	no	no	splenial absent	no	?

the ascending process of the left maxilla, together with a differentiation of nasal and prefrontal sutural surfaces on the frontal, indicates that both the nasals and prefrontals were similar in form and extent to *Elseya* and *Emydura*. The ventral ridges of the frontal bones are vertical rather than turned inwards into close approximation. No premaxilla or vomer are preserved, and the maxillae are damaged anteriorly and medially. Thus, it is not possible to establish the shape of the premaxillae, whether palatal intermaxillary or else premaxillary-vomer contact occurred, what the shape of the internal narial aperture was, or where the prepalatal foramina were positioned.

The triturating surface of the maxillary palate is bounded by a well-developed labial ridge, but the lingual ridge is weakly expressed, and no medial ridge is present. The lateral ascending processes do not make contact on the dorsal surface of the skull with the frontals. The palatal bones just come into contact with each other

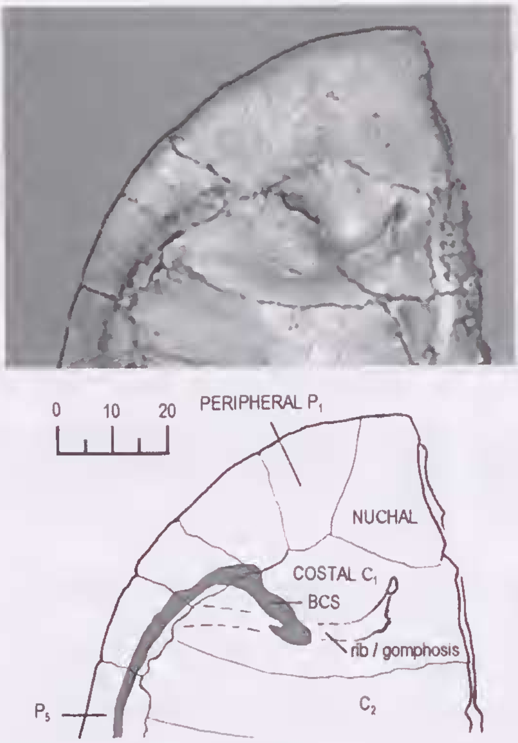


Fig. 7. *Birlimarr gaffneyi* gen. et sp. nov. holotype P9215-1. Internal view of left side of carapace showing form and position of bridge-carapace suture (BCS).

posteromedially, suggesting that the vomer either stopped short of, or else barely made contact with, the pterygoids. The palatine-pterygoid sutures are oriented posterolaterally at about 45° to the axial plane of the skull, and the interpterygoid suture is long in proportion to the basicondylar length of the cranium. The lateral trochlear processes of the right pterygoid (the left is missing) is quite short. In ventral view, the lateral margin of the processus trochlearis pterygoidei is straight. The ventral trace of the pterygoid-quadrate suture is long and also oriented at about 45° to the axial plane.

The most noteworthy features of the dorsal cranial surface are the sutural relationships between the frontals, postorbitals and parietals. The postorbital is quite large compared to *Elseya* and *Emydura*, but not as large as in *Pseudemydura*, appearing distinctly wider than long in dorsal view. The frontals have a medial posterior process, with the lateral segments of the frontal-parietal contacts diverging anterolaterally.

The mandible is represented by fused dentaries and both articulars and angulars, which is sufficient to give an overall indication of the mandibular shape (Fig. 10). The prearticulars and coronoids are missing, and thus the preservation does not indicate whether or not splenials were present. The mandible is almost as broad as it is long (greatest width/greatest restored length ca. 0.95) and lightly built. The rami are curved in dorsal and ventral views, forming a mandibular angle of about 50° (i.e. the angle between lines drawn from the tip of the symphysis to the articular facets - Legler and Cann 1980). Although the tip is damaged, the tomial profile in lateral view was clearly only moderately upcurved at the tip.

Cervical vertebrae. The Chelidae have the following unique pattern of cervical centrum articulations: (2(, (3(, (4(, (5),)6),)7(, (8) (Williams 1950, Gaffney 1979a). The P9215-1 cervical series includes complete or almost complete vertebrae 2 and 4-7, neural arch 8, and the left half of the axis neural arch with postzygapophyses missing (Fig. 11). There are two poorly preserved fragments with P9215-1 that might represent the centrum and neural arch of cervical 3. The cervicals of the fossil species are very similar to those of *Elseya denata*, though of slightly stockier proportions (Fig. 11). The cervical series has an estimated restored length of about 48 mm, which compares with an estimated length of 82 mm for the dorsal series, using the distance between the anterior- and posterior-most rib heads on the inside of the carapace.

Appendicular elements. The generally stockier proportions of *Birlimarr gaffneyi* gen. et sp. nov. relative to *Elseya dentata* are also evident in the appendicular skeletal elements selected for illustration (Fig. 12). Morphologically, they appear to be typically chelid when compared with the extant species at hand.

Numerous manus and pes elements, though certainly not the complete suite, are present in the type specimen, but no attempt

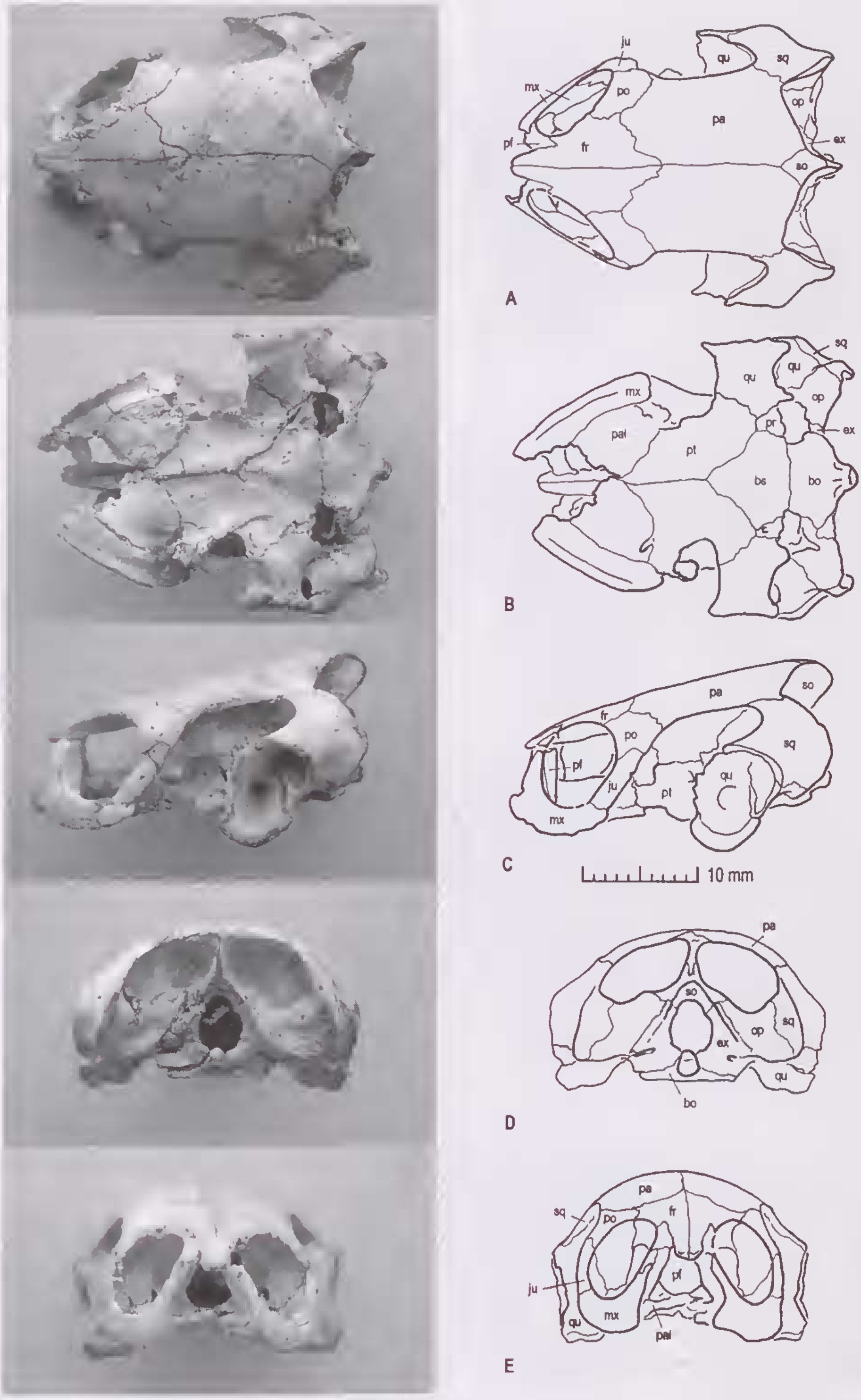
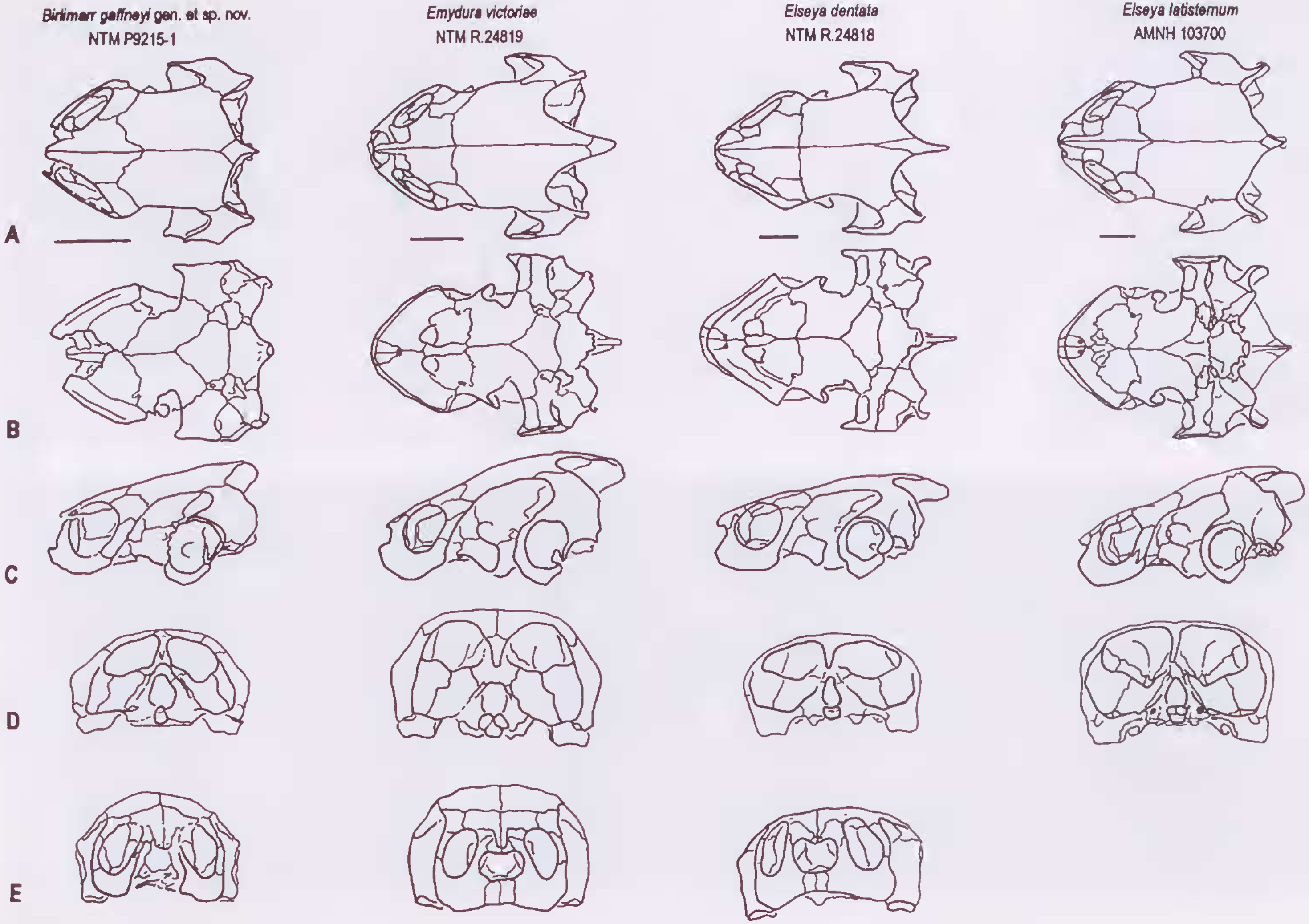


Fig. 8. *Birlimarr gaffneyi* gen. et sp. nov. holotype cranium, P9215-1 in **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, posterior; and **E**, anterior views.


Birlimarr gaffneyi gen. et sp. nov.
NTM P9215-1
Emydura victoriae
NTM R.24819
Elseya dentata
NTM R.24818
Elseya latisternum
AMNH 103700
A
B
C
D
E

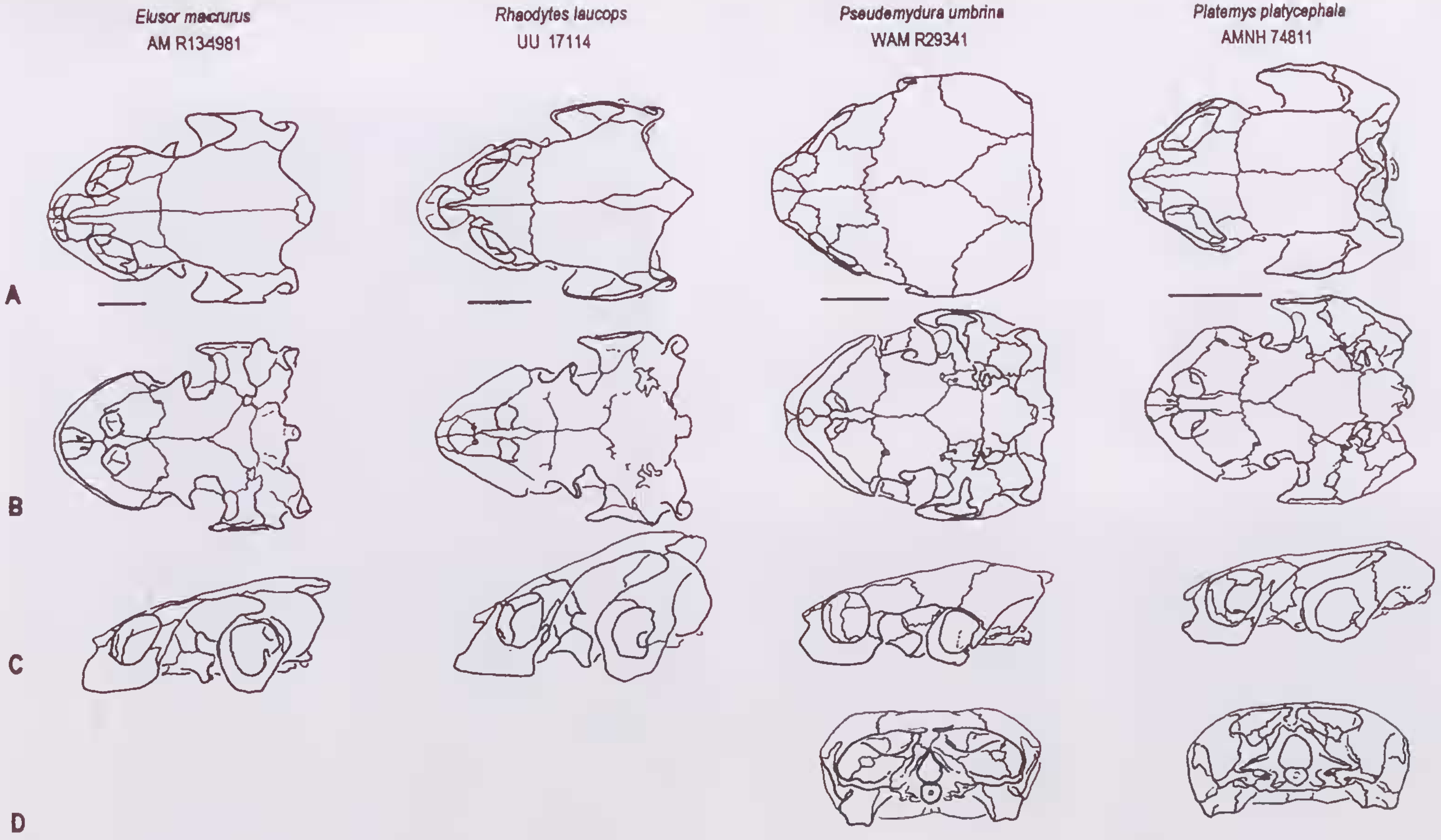


Fig. 9. Comparative cranial morphology of selected chelid species in **A**, dorsal; **B**, ventral; **C**, lateral; **D**, posterior; and **E**, anterior views. Scale bars equal 10 mm. *Elseya latisternum* after Gaffney (1977: fig. 7); *Elusor macrurus* after Cann and Legler (1994: fig. 6); *Rheodytes leucops* after Legler and Cann (1980: fig.2); *Pseudemydura umbrina* after Gaffney (1977: figs 1B,2B, 4B, 6B); and *Platemys platycephala* after Gaffney (1977: figs 1C, 2C, 4C, 6C).

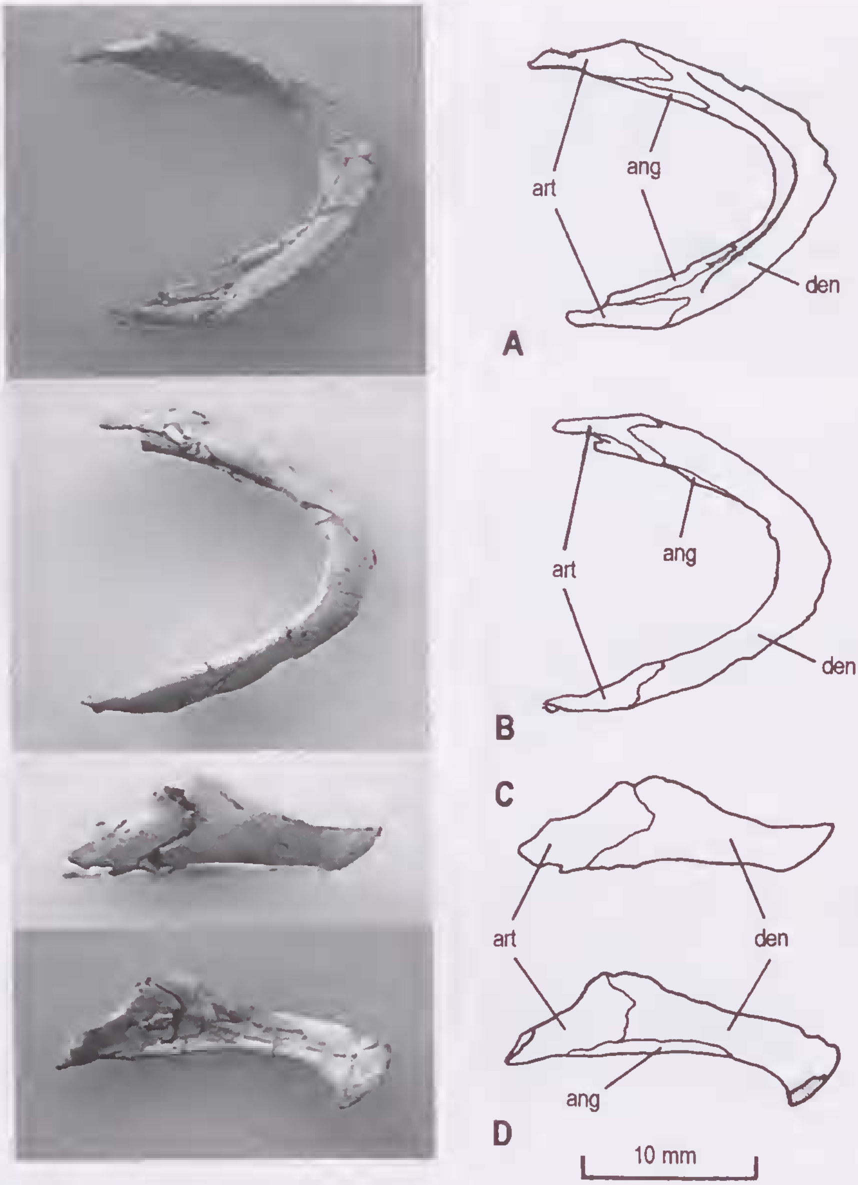


Fig. 10. *Birlimarr gaffneyi* gen. et sp. nov. mandible P9215-1 in: **A**, dorsal view; **B**, ventral view; **C**, right lateral view; and **D**, internal view of left ramus.

was made at reconstruction as they appear at present to be of only minor systematic utility, as outlined in the following section.

Comparative remarks. P9215-1 and referred material represents a small species of short-necked chelid. Lacking the diagnostic characters of *Pseudemydura*, its affinities are clearly with the Emydurodd. *Birlimarr gaffneyi* gen. et sp. nov. lacks the diagnostic shell and/or skull characters of *Rheodytes* and *Elusor*; but a unique suite of skull and carapace character states preclude its inclusion in *Emydura*, the *Elseya dentata* generic group, or the *Elseya latisternum* generic group (Tables 1-3). It is therefore placed in its own genus, *Birlimarr* gen. nov.

The phylogenetic relationships of *Birlimarr* gen. nov. to other short-necked genera are investigated below.

The pterygoid of *Birlimarr gaffneyi* gen. et sp. nov. is not identical in shape to any other chelid examined. The anterior suture with the palatine is almost straight, and oriented at 45° to the axis. In other chelids it is variously straight or concave forward, but perpendicular or sub-perpendicular to the axis (using the chord of the concavity where the suture is not straight). Another distinctive feature of *Birlimarr gaffneyi* gen. et sp. nov. is the length and anterolateral orientation, in ventral view, of the pterygoid-quadrate suture. In other forms, this suture appears to extend laterally from the pro-otic before swinging anteriorly at right angles towards the posterior face of the temporal fossa, medial to the articular surface for the mandible. No phylogenetic significance can be attached to these features at this stage, but they help diagnose the new genus and species.

The only previously described mid Tertiary fossil forms that appear to have any particular similarities to *Birlimarr gaffneyi* gen. et sp. nov. are QM F31304 from Melodies Maze Site, Miocene Carl Creek Limestone of Riversleigh, western Queensland (White 1997), and '*Emydura* sp.' from the Oligocene or Miocene of Taroona, Tasmania described by Warren (1969). The Queensland specimen (White 1997: fig. 2) is accompanied by a highly schematic interpretation of the carapacial scute pattern (White 1997: fig. 3), which at first glance suggests a form quite distinct from *Birlimarr gaffneyi* gen. et sp. nov., partly, as pointed out to us by S. Thomson, because 13 marginal scutes per side are depicted. Thirteen marginal scutes in QM F13304 would seem to be a misinterpretation (Fig. 13), being otherwise only known in the Tribe Carettini of the Cheloniidae, which has both an extra marginal scute and peripheral bone (Zangerl 1969; Gaffney and Meylan 1988).

Amongst the similarities between P9215-1 and QM F31304 (Figs 5, 13, 14) are: small adult size (approximate carapace length: P9215-1, 160 mm; QM F31304, 100 mm); vertebral scute pattern; proportionally large nuchal (as indicated by negative space in QM F31304); regular oval outline with no flare over the hindlimbs; and broad, well-defined, parallel-sided bridge carapace

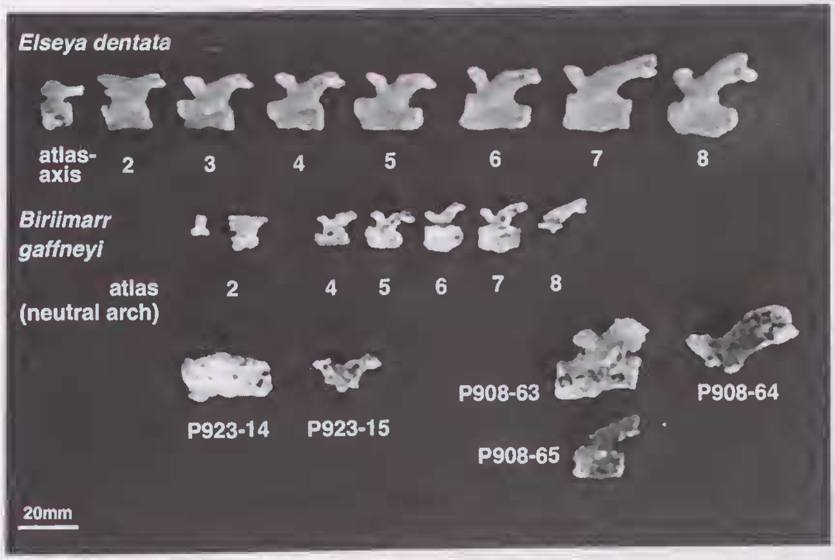


Fig. 11. Cervical vertebrae of *Birlimarr gaffneyi* gen. et sp. nov. (P9215-1) compared with an *Elseya dentata* series (R.24818) and various isolated fossil cervicals. P923-14 (Site X), procoelous centrum, therefore cervical 2, 3 or 4; P923-15 (Site X), neural arch most closely resembling cervical 4 of *E. dentata*; P908-63 and P908-65 (Blast Site), vertebrae with biconcave centra, therefore cervicals 7; P908-64, neural arch most closely resembling cervical 8 of *E. dentata*.

Table 2. Comparison of carapacial seam contacts (following Legler and Cann 1980, after Tinkle 1962). The formula indicates the position at which interlateral scale seams contact marginals scales: seam A = pleural 1 – vertebral 1 seam; seams B,C,D = 3 interpleural seams, anterior to posterior; seam E = pleural 5 – vertebral 5 seam. The letters A (anterior), M (medial), and P (posterior) appended to the marginal scute number indicate the position of seam contact on the marginal. *Rheodytes* is unique (autapomorphous) in having seams C and D contacting scales 6 and 8, in contrast to the usual condition of contact with marginals 7 and 9. * indicates Oligocene or Miocene fossil material.

Taxon / specimen	Source	Carapacial seams				
		A	B	C	D	E
**Birlimarr gaffneyi* gen. et sp. nov. NTM P9215-1	Figs 5, 14	2M	5A	7M	9M	11A
All *Elseya* spp and *Emydura* spp	Cann and Legler 1980	2	5	7	9	11
Rheodytes leucops	Legler and Cann 1980	2M	5A	6P	8P	11A
Elusor macrurus	Cann and Legler 1994: fig. 1	2M	5M	7M	9A	11A
* '*Emydura* sp.' UCMP 77348, Wipajiri Ftn	Fig. 14 (Gaffney 1979: fig. 12)	2M	5M	7M	9M	11A
*'*Emydura* sp.' NMV P159937 Namba Ftn	Fig. 14 (Burke *et al.* 1983: fig. 2)	2M	5M	7M	9M	11A
*'*Emydura* sp.' Tasmania UTG 86978	Fig. 14 (Warren 1969: fig. 1)	2M	5M	7P	9A	11M
*'Genus indet. A' QM F13304 Carl Creek Lst	Figs 13, 14 (White 1997: fig. 2)	2M	5M-	7P	9A	11A

suture on the internal surface of costal 1. However, unlike the P9215-1 carapace, QM F13304 is low and flat, there is an axial depression, peripherals 3, 4, 5 and part of 6 curve ventrally so that the carapace margin is rounded onto the bridge, and there is a prominent, ventrally-projecting crest between the rib head and the medial margin of the bridge carapace suture on pleural 1 (White 1997). White (1997) concluded that QM F31304 could not be placed in any of the extant chelid genera, and consequently designated it 'Genus indet. A'. It is here referred to cf. *Birlimarr* sp. indet., on the basis of the similarities listed above.

Birlimarr gaffneyi gen. et sp. nov. also has some similarities to the chelids described by Warren (1969) from the Oligocene or Miocene of Tasmania, referred to *Emydura* sp., in: small adult size; similar vertebral scale pattern; and apparent lack of flaring over the hind legs (Fig. 14 - note that some distortion of the shell is evident). However, the plastron of the Tasmanian form, of which a composite reconstruction of three individuals is depicted, differs from *Birlimarr gaffneyi* gen. et sp. nov. in having much slimmer proportions and smoothly tapering anterior and posterior lobes. There are insufficient data available to make a new judgement about the generic affinities of Tasmanian fossils.

Other described Miocene carapaces (Fig. 14) differ from *Birlimarr gaffneyi* gen. et sp. nov. in their considerably greater adult size and contrasting vertebral scale pattern, as well as in other osteological details that are discussed below under comparative remarks for gen aff. *Elseya/Emydura* sp. indet. Fragmentary '*Emydura* sp.' skull material

Table 3. Comparison of plastral formulae, after Legler and Cann (1980). The formulae indicate the relative interlaminal lengths of plastral scales. The preservation of *Birlimarr gaffneyi* gen. et sp. nov. (P9215-1) permits only measurements from the left to be taken (Fig. 5). It appears that only in *Birlimarr gaffneyi* gen. et sp. nov. and *Elusor* is the pectoral scale longest, and only in *Birlimarr gaffneyi* gen. et sp. nov. and the *Elseya latisternum* group is the femoral not amongst the three longest scales. * indicates Oligocene or Miocene fossil material.

Taxon / specimen	Source	Plastral formula
**Birlimarr gaffneyi* gen. et sp. nov. NTM P9215-1	Figs 5, 14	pectoral (33.0 mm) > abdominal (28.8 mm) > intergular (26.5 mm) > femoral (23.3 mm) > anal 21.2 (mm)
Elseya dentata group	Legler & Cann 1980: table 1	femoral > pectoral > abdominal(50%): femoral (79%) or pectoral (21%) longest
Elseya latisternum group	Legler & Cann 1980: table 1	anal > pectoral > intergular (24%): anal (73%), femoral (10%) or pectoral (10%) longest
Emydura spp	Legler & Cann 1980: table 1	pectoral > femoral > abdominal (48%): pectoral (78%) or femoral (21%) longest
Elseya georgesi	Cann 1997	femoral>intergular>anal>humeral
Elseya irwini	Cann 1997	femoral > pectoral > abdominal > anal
Rheodytes leucops	Legler & Cann 1980: table 1	femoral > pectoral > anal (41%): femoral always longest (100%)
Elusor macrurus	Cann & Legler 1994	pectoral > femoral > anal or (pectoral ~= femoral) > anal
*'*Emydura* sp.' Tasmania UTG 86978	Fig. 14 (Warren 1969: fig. 1)	femoral > abdominal > anal ~= humeral ~= pectoral
* '*Emydura* sp.' UCMP 77348, Wipajiri Ftn	Fig. 14 (Gaffney 1979: fig. 13)	femoral > pectoral > intergular > abdominal > anal

associated with the Miocene Etadunna Formation carapaces are very similar to extant *Emydura macquarrii* (Gaffney 1979a: figs 2-10), representing a larger species than *Birlimarr gaffneyi* gen. et sp. nov. The skull of the Etadunna Formation species is proportionally longer and narrower than *Birlimarr gaffneyi* gen. et sp. nov., as evidenced by length to width proportions of, for example, the parietals and basisphenoid. Furthermore, the frontals lack a posteromedial process; the postorbitals are proportionally small and longer than wide in dorsal view; and the supraoccipital extended posteriorly beyond the level of the occipital condyle (Gaffney 1979b: figs 5A, 7A). Thus, to the extent that comparisons are possible, *Birlimarr gaffneyi* gen. et sp. nov. differs from Miocene *Emydura* sp. material from South Australian deposits in the same respects as it does from extant *Emydura* spp.

Birlimarr gaffneyi gen. et sp. nov. shows the typical 'short-necked' condition in which the cervical vertebral series is shorter than the dorsal series. Gaffney (1979a) interprets the condition of the cervical series being longer than the dorsals as a synapomorphy of the subtribe Chelina (Fig. 1). P9215-1 would appear to be one of the few Australian fossil specimens in which this particular character can be assessed. Atlas-axis morphology appears to be of utility and

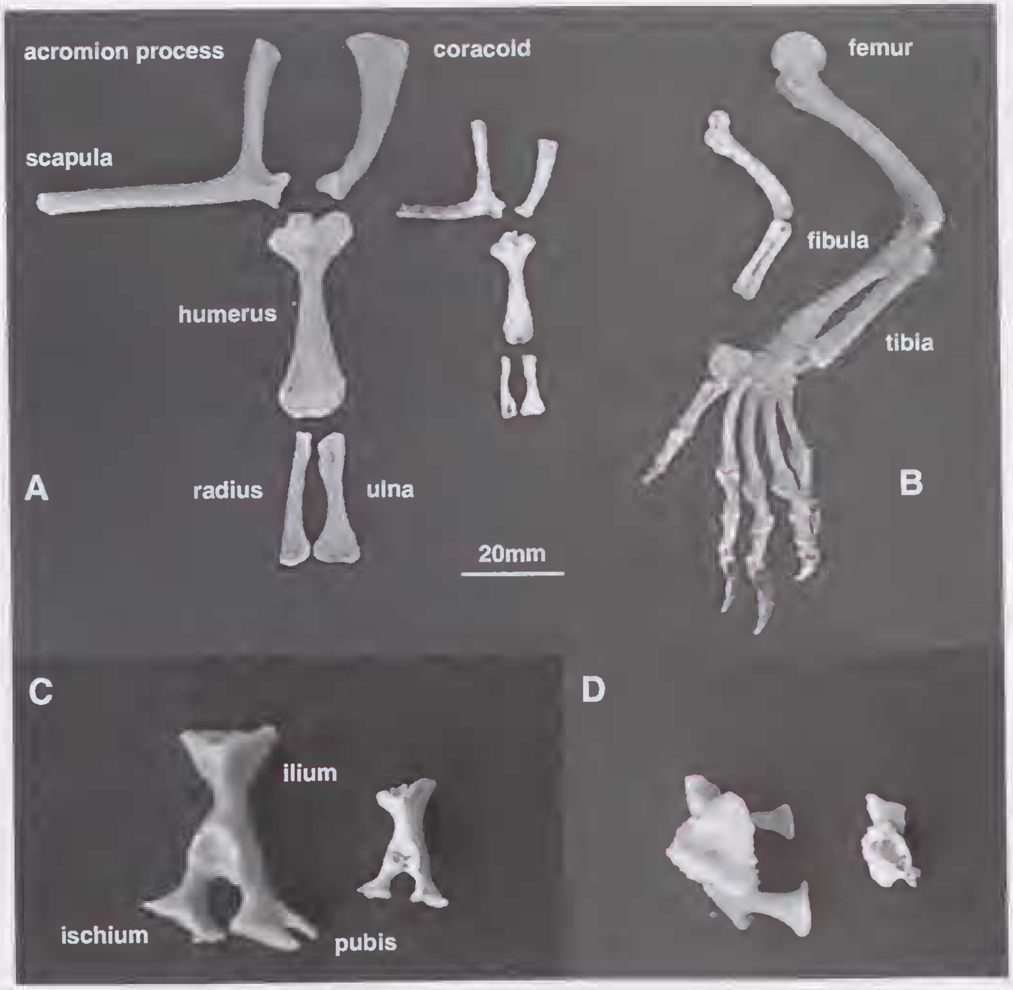


Fig. 12. Appendicular elements of holotype *Birlimarr gaffneyi* gen. et sp. nov. (P9215-1) compared with *Elseya dentata* (R.24818). The fossil is the smaller individual. **A**, disarticulated right forelimbs, in dorsal view (scapula rotated into the plane of the other elements); **B**, articulated left hind limbs in dorsal view; **C**, left innominates in lateral view; **D**, left innominates in dorsal view, anterior to the top.

further potential in the resolution of chelid phylogeny, exhibiting character states that can readily be interpreted as synapomorphies (Gaffney 1979a: 20-21). The atlas-axis complex of P9215-1 is represented only by the incomplete left neural arch of the atlas, and is very similar to that of *Elseya dentata*. The specimen is sufficient to determine two of the suite of primitive states found in *Elseya* plus *Platemys* (? plus *Pseudemydura*), namely that the atlas-axis zygapophyseal articulation is oriented ventrolaterally rather than horizontally; and that the atlantal elements were loosely articulated rather than fused.

At present, and perhaps mostly due to the lack of comparative studies, the appendicular skeleton of chelids is of minor systematic use. Gaffney (1979a) reports that *Chelodina* consistently differs from *Emydura* in having fused distal carpals 5 and 4 and sometimes also 3. No fused carpals were collected with P9215-1.

Etymology. Named *gaffneyi*, in recognition of Eugene Gaffney's (American Museum of Natural History) many

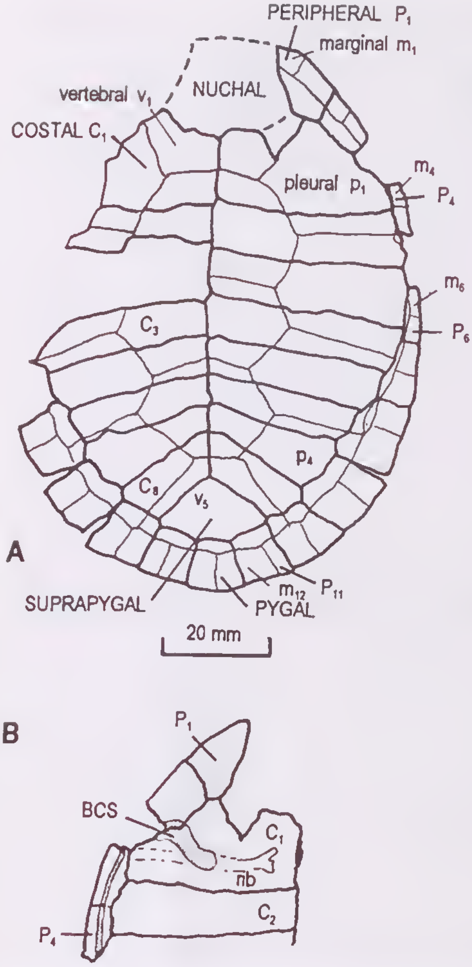


Fig. 13. Interpretative diagram of the osteology and scale pattern of the Miocene Carl Creek Limestone carapace QM F31305. **A**, dorsal view; **B**, internal view of the right anterior portion showing the morphology of the bridge – carapace suture BCS (after White 1997: fig.2).

contributions to Australian vertebrate palaeontology.

Genus aff. *Emydura/Elseya* sp. indet.

(Figs 15-18, Tables 1-3)

Reference specimen. P9464-134 (Top Site), incomplete carapace, and posterior lobe of plastron in which neither xiphiplastron is complete.

Referred material. P895-67 (Blast Site), anterior carapace fragment comprising the nuchal, left pleural 1 and left peripherals 1 to 3; P895-80 (Blast Site), nuchal; P9464-136 (Top Site), nuchal; P9464-155 (Top Site), right hypoplastron with anterior portion of xiphiplastron; P923-8 (Site X), left hypoplastron; P87106-17 + P925-6 (Site Y), right hypoplastron; P8692-23 (Blast Site), left hypoplastron; P923-7 (Site X), left pleural 1; P927-4 (Site Y), right costal 8.

Diagnosis. Large species of Emydurodd (up to 44 cm carapace length) most similar to extant species of *Emydura* and *Elseya*. Carapace evenly domed, lacking axial ridge, depression or flattening; probably evenly oval in outline rather than flared laterally over the hind legs. Posterior lobe of plastron tapering immediately behind the bridge (anterior lobe not known). Proportionally small cervical scute present on nuchal. First vertebral scute as wide as fifth, both wider than vertebrals 2, 3 and 4 which are about equal in width to each other. Vertebral 1 wider than long, vertebrals 2, 3 and 4 longer than wide, vertebral 5 probably about as long as wide. Interpleural seams intersect marginals 5, 7 and 9. Bridge carapace suture on pleural 1 diverges anterolaterally from trace of rib, well-defined sutural surface with sub-parallel anterior and posterior margins. Trace of rib on pleural 1 straight (no distal posterior curvature).

Description. The comparison below of isolated entoplastra suggests that two large species allied to *Emydura/Elseya* are present in the assemblage. Unfortunately the more informative anterior lobe of the plastron of the P9464-134 individual is not represented, and consequently this taxon can at this stage only be diagnosed by the carapace and posterior lobe of the plastron.

Carapace. P9464-134 has most of the paired bones of the carapace represented on one side or the other. Missing completely are peripherals 2, 3 and 10, and the pygal (Fig 15A, B). Peripherals 2 and 3 are, however, represented on referred specimen P895-67 (Fig. 16). The following observations of the general shape and dimensions of P9464-134 are based on the graphical reconstructions shown in Figure 15C. P9464-134 probably

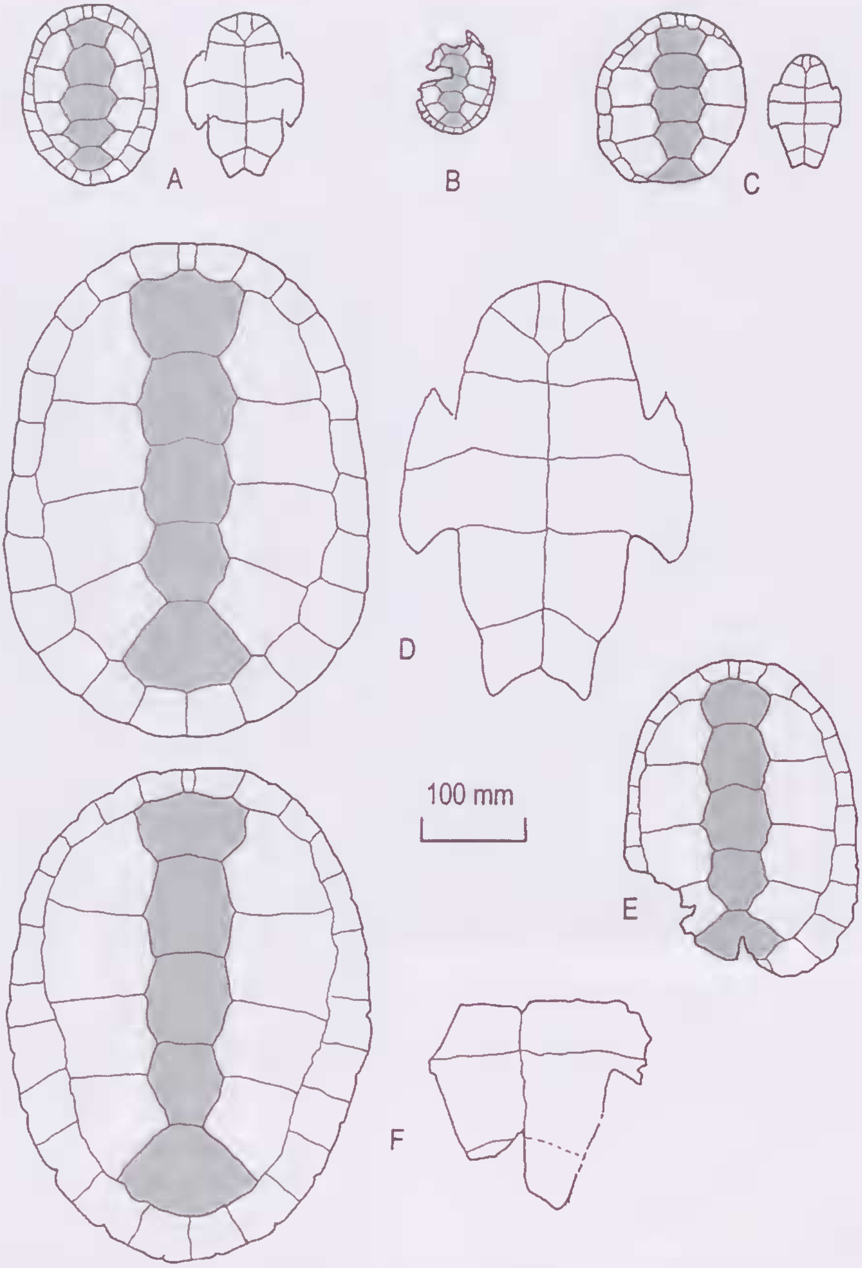


Fig. 14. Comparison of Oligocene and Miocene Emydurodd carapaces and plastra drawn to the same scale, vertebral scutes stippled. **A**, Miocene Camfield Beds of the Northern Territory *Birlimarr gaffneyi* gen. et sp. nov., NTM P9215-1; **B**, Miocene Carl Creek Limestone of Queensland, QM F13305, 'Genus indet A' (after White 1997: fig. 2 – see Figure 13 for details); **C**, Oligocene or Miocene of Taroona, Tasmania '*Emydura* sp.', carapace UTG 86978, plastron composite of MUZ 1204, 1205, and UTG 59374 (after Warren: 1969: fig. 1); **D**, Miocene Wipajiri Formation of South Australia, UCMP 77348, '*Emydura* sp.' (after Gaffney 1979: figs 12, 13); **E**, Miocene Namba Formation of South Australia, NMV P159937, '*Emydura* sp.' (after Burke et al. 1983: fig. 2); **F**, Miocene Camfield Beds of the Northern Territory, gen. aff. *Elseya/Emydura* sp. indet., NTM P9464-134.

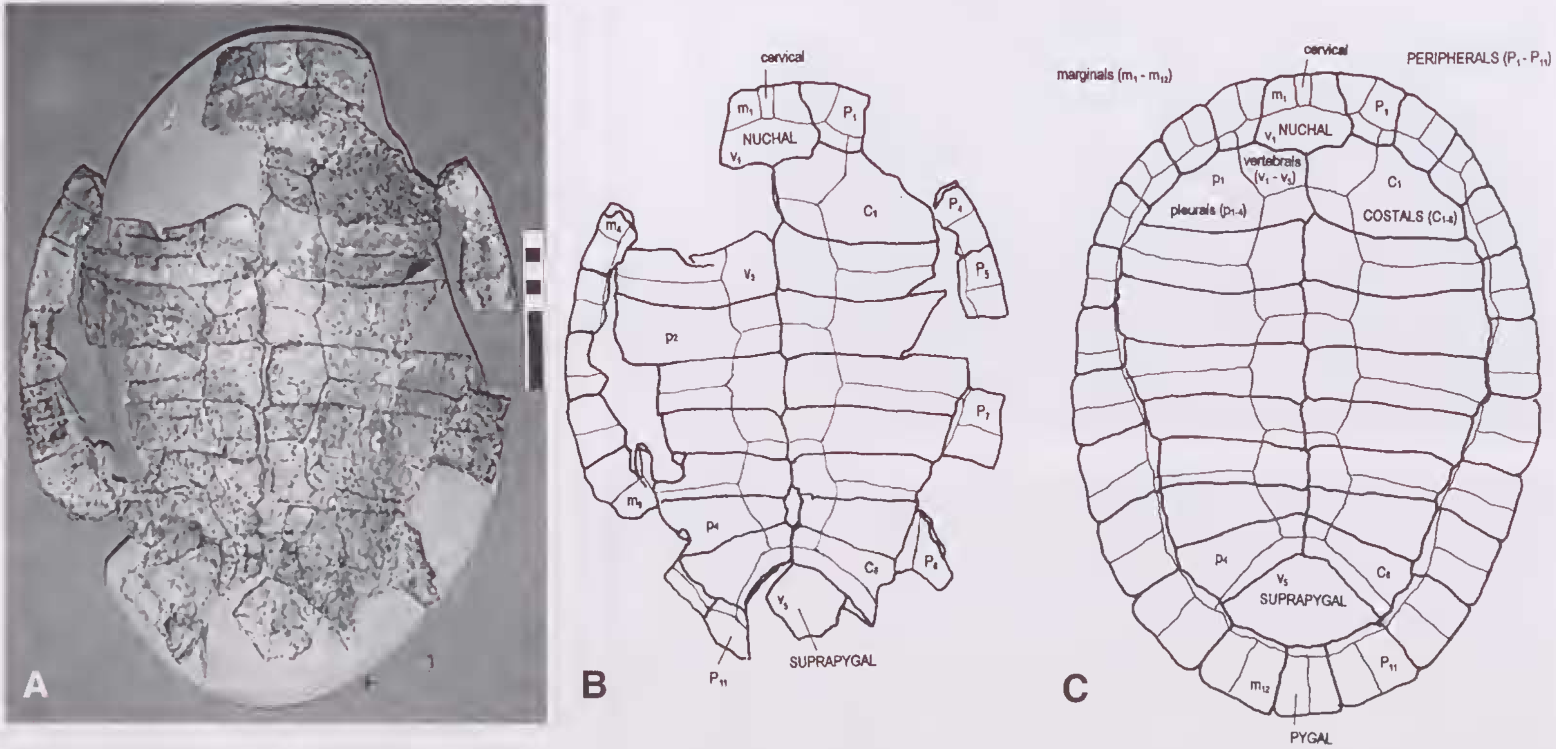


Fig. 15. Gen. aff. *Emydura/Elseya* sp. indet. P9464-134. **A**, dorsal view of carapace. **B**, interpretive diagram. **C**, restoration. Bones delimited by heavy lines and labelled in upper case, scutes delimited by fine lines and labeled in lower case. The two posterior peripherals of the specimen are highly abraded, a quite common feature in aged individuals. The restored outline of the posterior part of the carapace is therefore conjectural, but the outline of the whole carapace was clearly oval rather than flared laterally over the hind legs.

represents an aged individual, as evidenced by the heavily abraded posterior peripherals and extensive pathological modification of the surface of the shell. The effects of abrasion are conservatively compensated for in the graphical reconstruction in order to give an impression of what the likely shape and proportions of a more typical adult specimen of the species might have been.

In restored dorsal view (Fig. 15C), the carapace has a maximum estimated length of 44 cm, and maximum estimated width at about peripheral 7 of 30 cm. Although the posterior outline of restored shell is conjectural, there is little possibility that the carapace flared laterally over the hind legs. Any flaring would require remarkably wide peripherals at the level of the hind legs, and no such indicators are present amongst the many isolated posterior peripherals in the Bullock Creek LF assemblage. A notable feature of P9464-134 is the 'keyhole' outline of the pleurals plus suprapygal. This is a real feature, and definitely not attributable to distortion or displacement. Assuming that P9464-164 is not an aberrant example of the species, the indications are that the shell of this taxon was either regularly oval in outline as shown in Figure 15C, or possibly widest anteriorly and tapering posteriorly if the width of the posterior peripherals was fairly even. The carapace is smoothly domed, with no axial ridge or depression. Peripherals 4 to 7 are slightly upturned, with all other represented marginal bones very gently upswept.

A small cervical scute area is present on the nuchal. The first vertebral scute is wider than it is long. Vertebral 5 is about as long as it is wide, the width closely matching that of vertebral 1. In contrast, the intervening vertebrals are distinctly narrower than 1 and 5, and markedly longer than they are wide. The three intermediate vertebrals show a slight progressive reduction in size from anterior (vertebral 2) to posterior (vertebral 4). The interpleural seams intersect marginal scutes 5, 7 and 9 (Table 2).

The bridge carapace suture on pleural 1 (Figs 16, 17) is deep and well defined, diverging anterolaterally from the trace of the rib. The sutural area is just slightly wider medially than it is laterally.

Plastron. The plastron of the reference specimen, P9464-134, is represented by the hyoplastra and incomplete xiphiplastra (Fig.18). The proportions suggest that the whole plastron was narrow relative to its length. The posterior lobe begins to taper immediately posterior to the bridge, and the profile in ventral view of the femoral and anal scute areas is smoothly confluent, with barely any lateral bulge of the femoral area.

Comparisons made below of isolated hypoplastra support the notion that at least two large chelid species are present, but two or more forms amongst large xiphiplastra could not be discriminated. Larger hypoplastra showing evidence of taper immediately posterior to the bridge are tentatively referred to this taxon: *Chelodina* sp. B grows to at least moderately large size, but its hyoplastron is not known.

A proviso must be attached to the referral of P895-67 (Fig. 16) to this taxon. Associated with the specimen was a large hypoplastron, P895-66 (Fig. 19), which is determined below to represent a form of hypoplastron different from the reference specimen of gen. aff. *Emydura/Elseya* sp. indet., P9464-134. We suspect that P895-67 and P895-66 are the same individual, but cannot demonstrate that this is the case, and therefore have classified them independently.

Comparative remarks. At an estimated 44 cm straight-line carapace length, P9464-134 is amongst the largest recorded short-necked chelids (the referred specimens, P895-67 and P923-7, have larger dimensions than the homologous parts of P9464-134). The Miocene Wipajiri Formation *Emydura* sp. carapace, UCMP 77348, described by Gaffney (1979a) has a straight line carapace length of 44.5 cm. Of the larger extant short-necked turtles, the largest recorded *Elseya dentata* is 40 cm, *Emydura* sp. is 35 cm, and *Elusor* estimated at 40 cm (Cann and Legler 1994: table 2). The holotype of the extant species *Elseya lavarackorum* is a fossil with a restored carapace length estimated at 42 cm (Thomson *et al.* 1997). White (1997) reports that chelids up to 50 cm long are present in the Miocene Carl Creek Limestone, but it is not apparent whether these are short-necked forms or *Chelodina*. The largest *Chelodina* known to Cann and

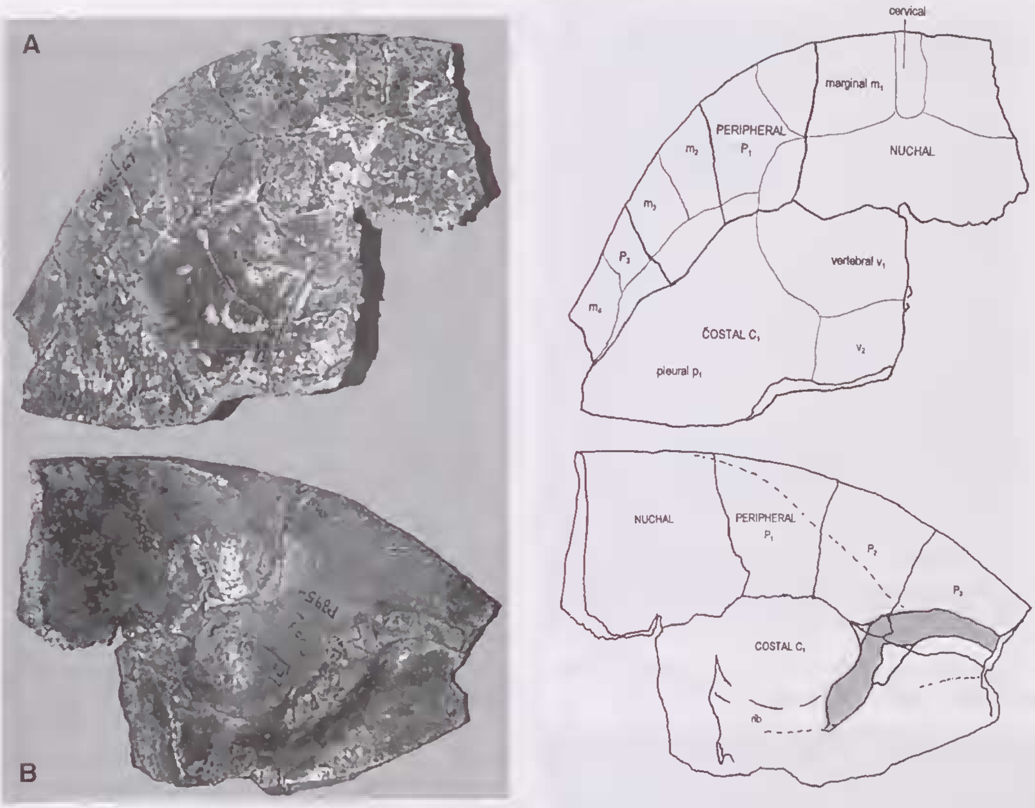


Fig. 16. Gen. aff. *Elseya/Emydura* sp. indet. referred specimen P895-67 in **A**, dorsal view; **B**, internal view showing relationships of scutes (lower case labels) and bones (upper case), and form and extent of the bridge carapace suture (BCS - stipple).

Legler (1994: table 2) is a '*C. (expansa)*' of 48.5 cm carapace length.

P9464-134 is similar to carapaces described from South Australian Miocene deposits (Fig. 14), in particular the Wipajiri Formation carapaces (UCMP 77348 and 72492) described by Gaffney (1979a), and the Namba Formation carapace (NMV P159937) described by Burke *et al.* (1983), in having the first vertebral scute wider than the second, though the difference is more pronounced in P9464-134 (see also referred specimen P895-67 - Fig. 16). Thompson *et al.* (1997) identify a first vertebral wider than the second (and third) as a diagnostic character of the *Elseya dentata* generic group (Fig. 20: character D). In all other short-necked chelids, the first vertebral is equal or sub-equal in width to the second vertebral. The bridge carapace suture on pleural 1 of NMV P159937 (Burke *et al.* 1983: fig. 2B) is of the same morphology as that of P9464-134. Thomson *et al.* (1997) indicate that this morphology is characteristic of *Rheodytes* and the Queensland *Elseya* species complex of the *Elseya dentata* generic group (Fig. 20: character B, state 2). All the Miocene carapaces compared here have the typical interlateral seam formula of short-necked chelids, rather than the unique state of *Rheodytes* (Table 2). While the indications from Thomson *et al.* (1997) are that the Miocene forms listed above may be allied to the *Elseya dentata* generic group, and possibly even to the Queensland *Elseya* species complex, none of the Wipajiri Formation maxillae described by Gaffney (1979) have the medial triturating ridge characteristic of *Elseya dentata*. This observation does not necessarily preclude the Miocene forms from an *Elseya dentata*

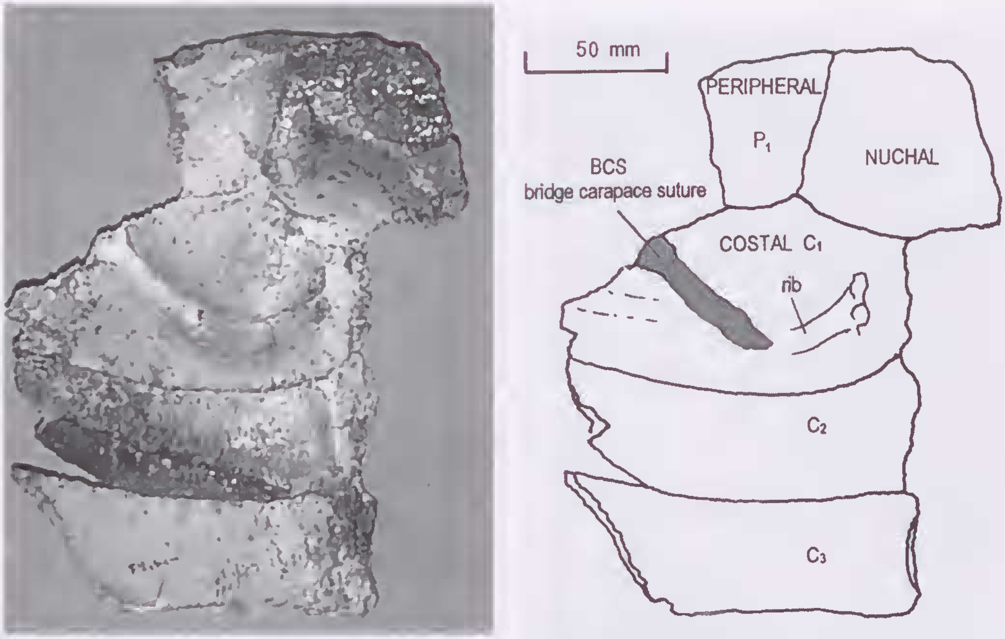


Fig. 17. Gen. aff. *Elseya/Emydura* sp. indet. reference specimen P9464-134, showing the form and shape of the bridge carapace suture on costal 1.

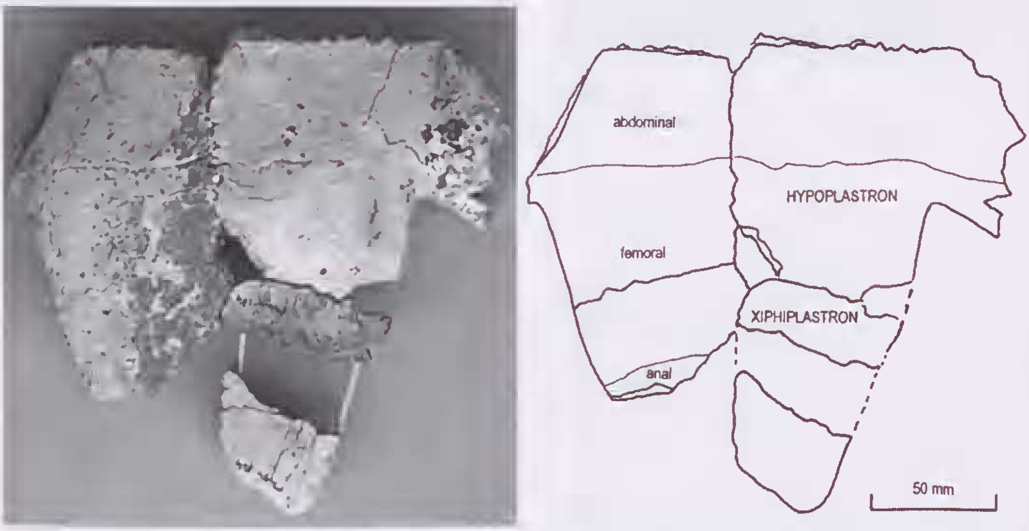


Fig. 18. Gen. aff. *Elseya/Emydura* sp. indet. reference specimen P9464-134, ventral view of the posterior plastral lobe.

generic group, but until the systematic significance of these skull and carapace characters are better understood, we prefer to designate P9464-134 and referred material to gen. aff. *Emydura/Elseya* sp. indet.

Several characters of the kind that are useful for distinguishing extant species suggest that P9464-134 and referred material may not be the same species as the South Australian forms (Fig. 14). In P9464-134 the

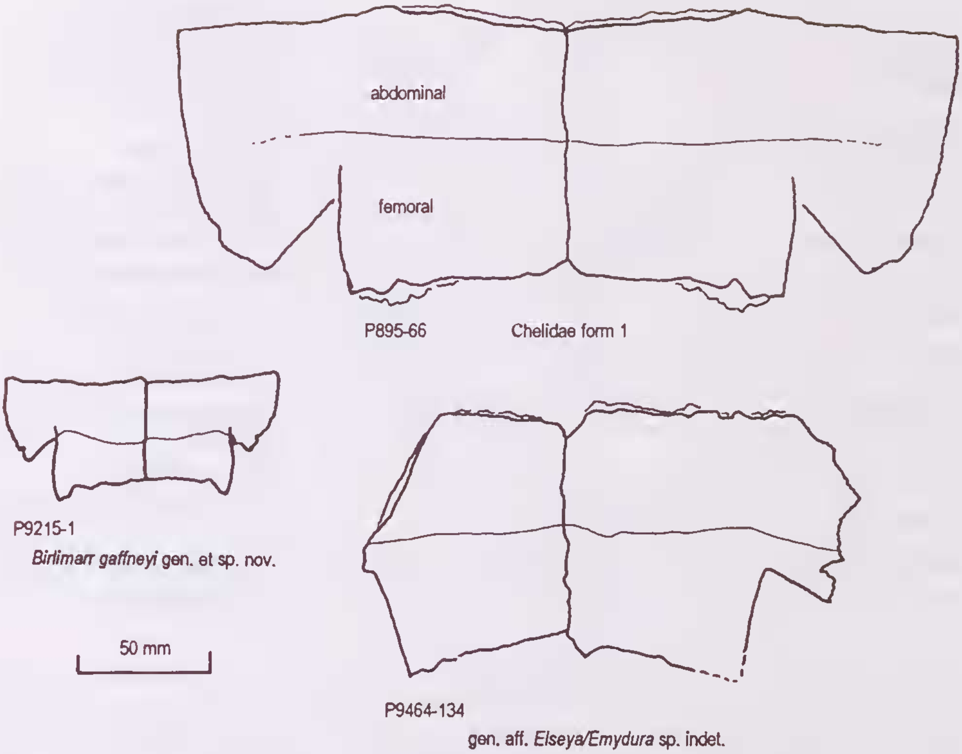

abdominal
femoral
P895-66
Chelidae form 1
P9215-1
Birlimarr gaffneyi gen. et sp. nov.
50 mm
P9464-134
gen. aff. *Elseya/Emydura* sp. indet.

Fig. 19. Hypoplastra. NTM P895-66 (Chelidae form 1) is mirrored.

first vertebral is proportionally shorter, vertebrals 2-4 are narrower, and the trace of the pleurals plus suprapygal is key-hole shaped rather than regularly oval. The South Australian carapaces flare out at about peripheral 8, but as indicated above, a flared margin was probably not a feature of the Bullock Creek form. Finally, the posterior plastral lobe tapers immediately posterior to the bridge, whereas the margins of the proximal posterior lobes of the South Australian examples are parallel.

Chelodd Gaffney, 1977
Chelodina sp. A
(Fig. 21, Table 4)

Reference specimen. NTM P908-49 (Blast Site), right epiplastron.

Referred material. None - other Bullock Creek LF *Chelodina* material described below from isolated bones cannot be assigned to *Chelodina* sp. A until more complete individuals are discovered.

Diagnosis. Diagnosed only by the epiplastron. A species of *Chelodina*, on the grounds that gular scutes are in medial contact anterior to intergular. Anterior margin of plastron describing a segment of a circle; width of intergular scute about one third width of plastron across epi-hyoplastral suture; parallel-sided portion of intergular extends unknown distance onto entoplastron.

Description. Epiplastron P908-49 comes from a relatively small turtle, but it is not possible to ascertain what stage of maturity the individual represented may have attained, and therefore what size the species may have grown to. The following description is based on a mirrored restoration of the specimen (Fig. 21), which gives a more complete impression of the form of the distal portion of the anterior plastral lobe of the species, and facilitates comparison with living species. The anterior margin of the restored plastron

	A	B	C	D	E
Pseudemydura umbrina	0	1	0	1	0
Elseya latisternum generic group	0	1	0	1	0/1
Elusor macrurus	0	1	0	1	0
Rheodytes leucops	1	2	0	1	0
Elseya dentata generic group	1	3	1	2	1
Elseya novaguineae	1	3	1	2	0
Queensland *Elseya* species complex	1	2	1	2	1
Elseya lavarackorum	1	2	1	2	1
Emydura	1	4	1	1	0
***Birlimarr gaffneyi* gen. et sp. nov.**	1	1	1	1	0

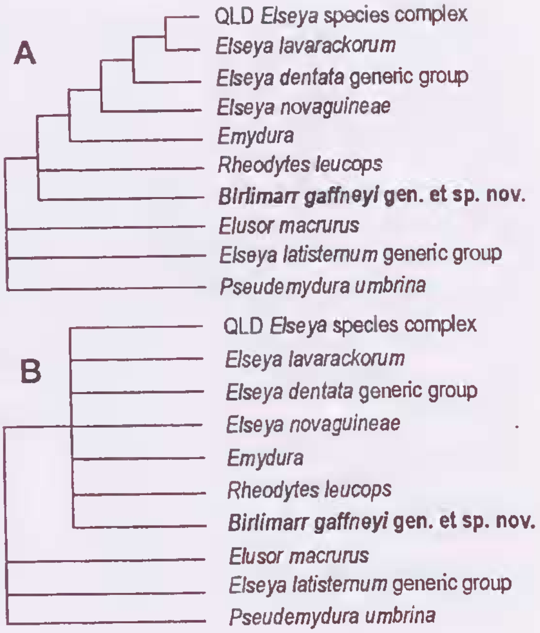

A
QLD *Elseya* species complex
Elseya lavarackorum
Elseya dentata generic group
Elseya novaguineae
Emydura
Rheodytes leucops
***Birlimarr gaffneyi* gen. et sp. nov.**
Elusor macrurus
Elseya latisternum generic group
Pseudemydura umbrina
B
QLD *Elseya* species complex
Elseya lavarackorum
Elseya dentata generic group
Elseya novaguineae
Emydura
Rheodytes leucops
***Birlimarr gaffneyi* gen. et sp. nov.**
Elusor macrurus
Elseya latisternum generic group
Pseudemydura umbrina

Fig. 20. Post-cranial character matrix after Thomson *et al.* (1997: table 1). Characters A to E are those of Thomson *et al.* but are expressed slightly differently here after clarification was sought from S. Thomsom. **Character A**, relationship of bridge carapace suture BCS to the trace of the rib on pleural 1: 0 = parallel and adjacent, 1 = anterolaterally divergent. **Character B**: BCS shape on pleural 1, ordered multistate: 1 = anterior and posterior edges diverge, widest distal to vertebral column, 2 = anterior and posterior edges essentially parallel, with prominent suture surface between them; 3 = prominent suture surface with marked medial constriction; 4 = sutural surface widest proximal to vetebral column, constricting distally to form a ridge, i.e. essentially no sutural surface distally. **Character C**: rib morphology, pleural: 0 = distal part of rib inflected posteriorly, rib rotated along its axis; 1 = no distal posterior inflection, no axial torsion (axial rotation of the rib may only be apparent if the tip is free of the peripheral gomphosis). **Character D**, relative widths of vertebral scales, unordered: 1 = vertebrals 1 to 3 equal or sub-equal, 2 = vertebral 1 wider than 2 and 3. **Character E**: cervical scute: 0 = usually present, 1 = usually absent. Consensus trees of **A**, two equally short trees, state 1 of Character D set as plesiomorphic; **B**, 24 equally short trees, state 2 of Character D set as plesiomorphic (Hennig86, Version 1.5 – Farris 1988). Identical results obtained whether Character E of *Elseya lavarackorum* generic group set at 0 or 1.

describes an arc of a circle, but not quite a complete semi-circle. Medial contact of the gular scutes anterior to the intergular is diagnostic of *Chelodina*. The intergular occupies less than one third of the posterior width across the combined epiplastra. The parallel lateral margins of this scute extended onto the entoplastron, and no part of its contact with the pectorals is present on the epiplastra. The pectoral scutes are represented on the posteromedial extremities of the epiplastra, the humeral pectoral contacts thereby intersecting the epi-hyoplastral sutural surface.

Comparative remarks are made below under *Chelodina* sp. B.

Chelodina sp. B
(Fig. 21, Table 4)

Reference specimen. NTM P9272-4 (Blast Site), left epiplastron.

Referred material. NTM P9464-147 (Top Site), right epiplastron; P895-72, (Blast Site),

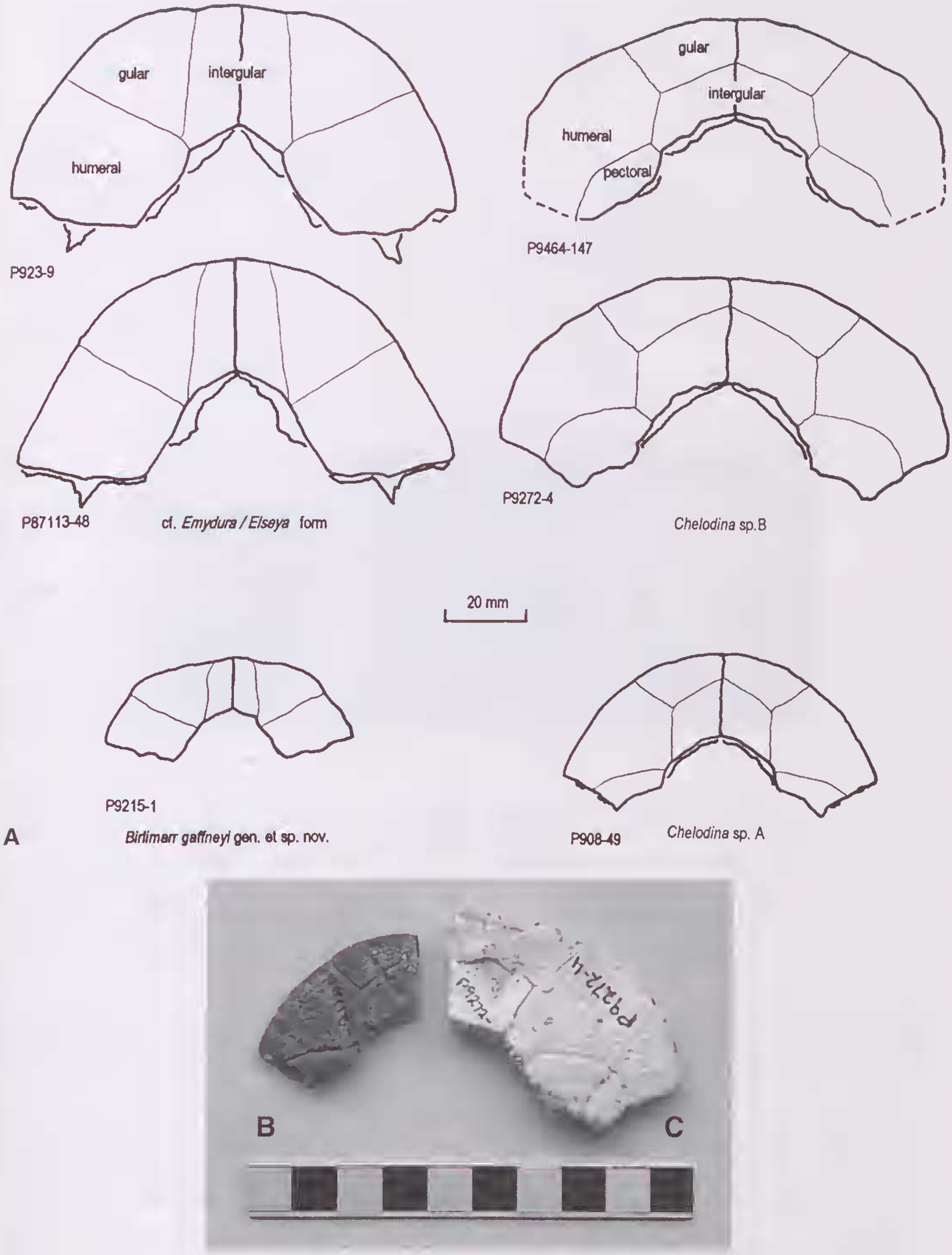


Fig. 21. Epiplastra. **A**, forms of epiplastra present in the Bullock Creek LF assemblage. Excepting *Birlimarr gaffneyi* gen. et sp. nov. P9215-1, each of the other specimens is mirrored. **B**, *Chelodina* sp. A reference specimen, P908-49. **C**, *Chelodina* sp. B reference specimen, P9272-4.

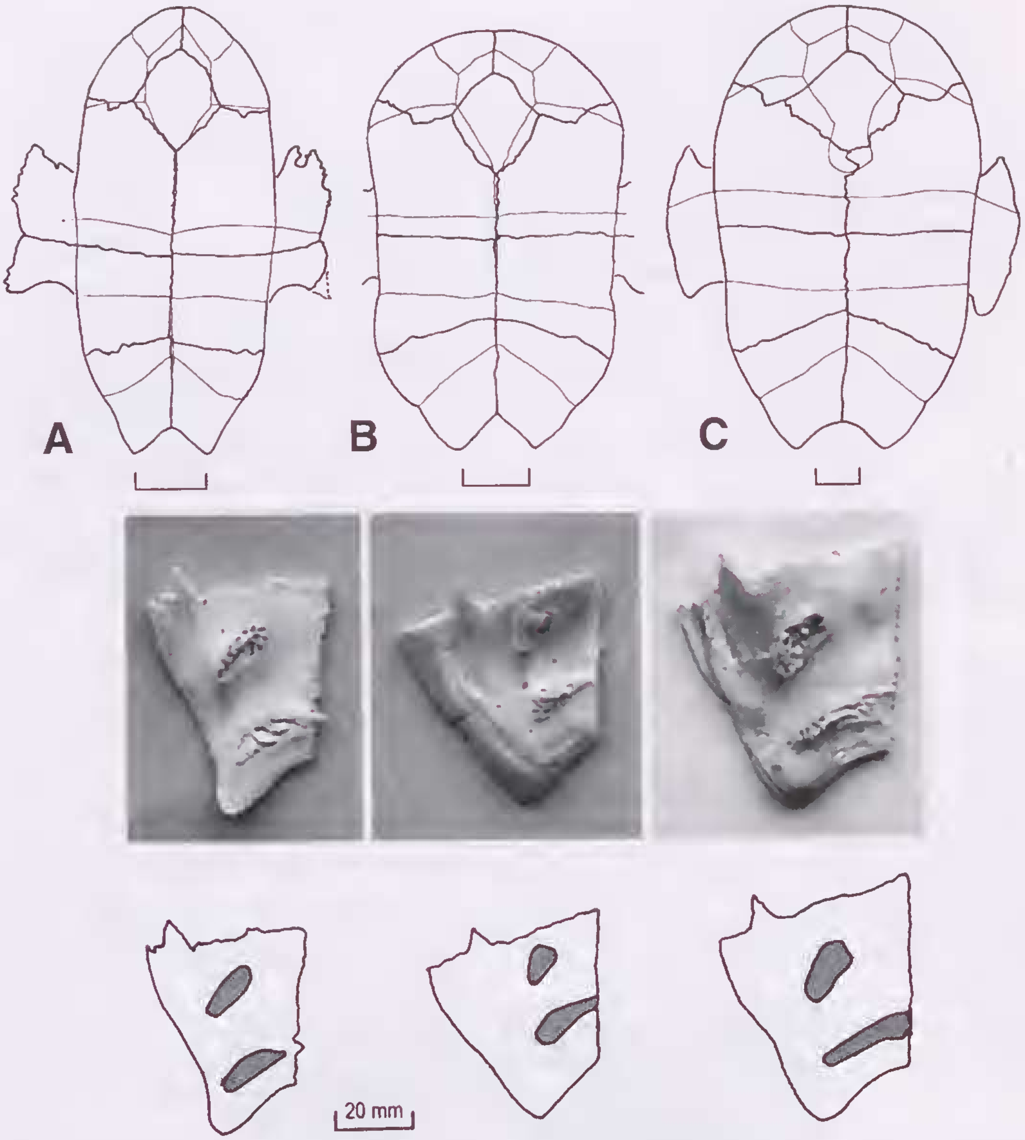


Fig. 22. Relationship of epidermal scales to bones in the plastra of selected extant *Chelodina* spp. and internal detail of the xiphiplastron: A, *C. rugosa* (R.24812); B, *C. longicollis* (R.24812); C, *C. novaeguineae* (R.16325). Individual elements can be identified by reference to Figure 5.

left epiplastron. No other Bullock Creek LF *Chelodina* material described from isolated bones can be assigned to *Chelodina* sp. B until more complete individuals are discovered.

Diagnosis. Diagnosed only by the epiplastron. A species of *Chelodina*, on the grounds that gular scutes are in medial contact anterior to intergular. Anterior margin of plastron squared off, rather than smoothly arced; width of intergular scute greater than one third width of plastron across epi-hyoplastral suture; parallel-sided portion of intergular entirely on entoplastra, tapering posteriorly an unknown distance onto entoplastron.

Description. As for *Chelodina* sp. A, the following description is based on a mirrored restoration of the specimen, in order to give

Table 4. Epiplastra – measurements and classification. Measurements in italics are estimates.

	Birlimarr gaffneyi gen. et sp. nov.				cf. *Elseya/Emydura* form			*Chelodina* sp.A	*Chelodina* sp.B		
	L	R	L	L	L	R	R	R	L	R	L
	P9215-1 holotype		P9612-2	P906-22	P923-9	P87113-48	P87103-51	P908-49 reference	P9272-4 reference	P9464-147	P895-72
Intergular extends to anterior free margin of plastron	yes	yes	yes	yes	yes	yes	yes	no	no	no	no
L1	11.8	11.8	13.1		28.4	26.2	*40.0*	17.2	25.5	22.1	22.5
L2	25.3	*25.7*	26.9		51.4	49.2		36.3	50.4	*47.1*	
W1	27.3	29.8	*32.0*		53.8	50.0		36.8	53.6	49.5	
W2	17.4	18.1	*18.0*	19.7	31.5	28.5		15.3	22.7		
L1/W1	0.43	0.40	0.41		0.53	0.52		0.47	0.48	0.45	
L2/W1	0.93	0.86	0.84		0.96	0.98		0.99	0.94	0.95	
L1/W2	1.47	1.53	1.37		1.11	1.09		0.89	0.89		
L2/W2	1.45	1.42	1.49		1.63	1.73		2.37	2.22		
L1/L2	0.47	0.46	0.49		0.55	0.53		0.47	0.51		
Number of assigned individuals											10
Number of unassigned specimens											3
Minimum number of individuals											13

a more complete impression of the anterior portion of the plastron (Fig. 21).

Chelodina sp. B grew to a size comparable to that of the larger Emydurodd species in the assemblage. The anterior margin of the plastron is not smoothly arced, rather the progression is from a straight medial segment, to a gently arced intermediate segment, to a strongly (posteriorly) curved anterolateral segment. The anterior plastral lobe therefore has a somewhat squared-off profile, in which the margins of the posterolateral extremities of the epiplastra come close to being parallel to each other. *Chelodina* sp. B has the gular-intergular relationship diagnostic of the genus. The marginal parts of the parallel-sided portion of the intergular is entirely on the epiplastra, such that a small part of the postero-medially aligned pectoral-intergular contact is present on the epiplastra. The widest part of the intergular is a little greater than one third of the combined posterior width of the epiplastra. The pectoral humeral contacts cross the epi-hyoplastral sutural surface posteriorly.

Comparative remarks. The proportions of the two Bullock Creek *Chelodina* species are not much different (Table 4). However, *Chelodina* sp. A can be distinguished from *Chelodina* sp. B by its: rounded as opposed to squared off marginal profile of the anterior plastral lobe in ventral view; proportionally long inter-epiplastral contact; and proportionally narrower intergular. *Chelodina* sp. A has an epiplastral scute pattern similar to that of *Chelodina rugosa*, whereas that of *Chelodina* sp. B more closely resembles *C. novaeguineae* and *C. longicollis* in which the widest part of the intergular is entirely on the epiplastra (Fig. 22). P908-49 (*Chelodina* sp. A) resembles the epiplastron of *Chelodina* sp. QM F17415 from the Miocene Carl Creek Limestone described by Gaffney *et al*. (1989: fig. 2).

DESCRIPTION AND COMPARISONS OF ISOLATED AND INDIVIDUAL BONES

Introductory remarks. Small specimens that can only be interpreted as hatchlings or sub-adults are not assigned below to any form or referred to any of the taxa diagnosed above. Insufficient data have been published on sexual dimorphism and individual variability in Australian chelids to make any secure judgements about whether some of the recognised forms might represent the two sexes of the same species or possibly variants of a single morphospecies, and this issue receives no further attention at this time. The bones discussed below are those that were found to be most informative about possible species diversity amongst the entire Bullock Creek LF assemblage.

Epiplastra. Four forms can be distinguished on the basis of epiplastra: *Birlimarr gaffneyi*; a cf. *Elseya/Emydura* form; and *Chelodina* sp. A and sp. B. (Figure 21; Table 4). In the two *Chelodina* species, the intergular does not extend to the anterior margin, the gulars therefore coming in contact with each other at the midline, and the anterior part of the pectoral scute is present.

Birlimarr gaffneyi and the cf. *Elseya/Emydura* form have similar scute patterns, the gulars being entirely separated by the intergular with no part of the pectoral present, but they differ significantly in their proportions. *Birlimarr gaffneyi* has a proportionally short inter-epiplastral contact; the epiplastra are wide in proportion to their total length; the ventral profile is more strongly squared off; and the negative space for the anterior half of the entoplastron is proportionally short and wide. The two figured examples assigned to the cf. *Emydura/Elseya* form differ somewhat from each other. P923-9 has a more squared off ventral profile, compared to that of P87113-41 which is more smoothly arched. In the former, a small part of the humeral-intergular trace is present and the epi-hyoplastral suture is not as straight. However, these differences are not sufficient to propose that two similar but distinct forms are represented.

Entoplastra. Four forms are recognised amongst the sample of entoplastra (Table 5): *Birlimarr gaffneyi* (Fig. 5); cf. *Birlimarr* form; and cf. *Elseya/Emydura* forms 1 and 2 (Fig. 23).

Amongst Australian chelids, the intergular entirely separates the humerals and the anterior portion of the pectorals only in *Pseudemydura* and *Chelodina* (Gaffney 1977: table 3). In *Chelodina* the intergular covers almost the entire entoplastron, the intergular-pectoral grooves lying just medial to the ento-hyoplastral suture and coming together at the posterior tip of the entoplastron or extending onto the hyoplastra (Fig. 22). None of the isolated entoplastra of the Bullock Creek sample show these characters.

In *Birlimarr gaffneyi* the entoplastron is slightly wider than it is long, the intergular extends posteriorly for more than half the length of the bone, the interhumeral contact is short, and the anteromedial corners of the pectorals are present at the posterior margin. P907-44 matches in all these respects; P87103-48 differs only in that the intergular is shorter and the interhumeral contact longer. P87113-45 is just about as wide as it is long, the posterior tips of the gulars are present at the anterolateral margins, and the intergular extends posteriorly to about half way, but there is no trace of the pectorals. P907-44 and P87103-48, in spite of their similarity to the cf. *Birlimarr* form, cannot be assigned to that species on account of their considerably greater size, and are consequently assigned to cf. *Elseya/Emydura* form 1.

P87113-45 may represent an example of *Birlimarr gaffneyi*, but could conceivably also represent another species. It is assigned to cf. *Birlimarr* form on the grounds that there are no intermediate morphotypes which support its referral to the new species. A hyoplastron (P87103-50) of another individual conforms to P87113-45, adding weight to the possibility that another small

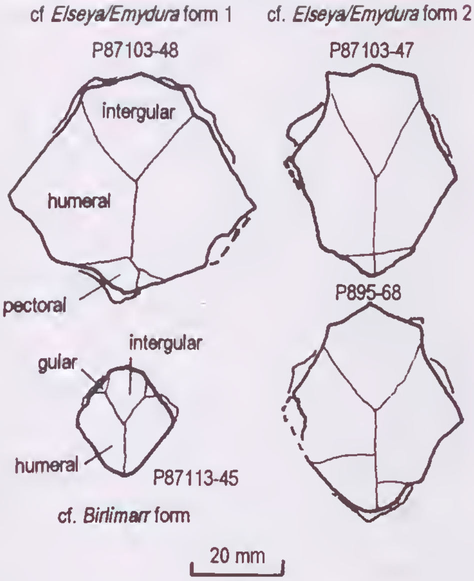
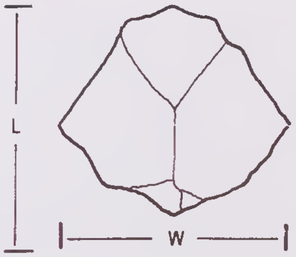


Fig. 23. Entoplastra.

Table 5. Entoplastra – measurements and classification. Measurements in bold = 2 x half-width. P9464-156 is determinate, but not measurable in the scheme used.



	Birlimarr gaffneyi gen. et sp. nov.			cf. *Birlimarr* form	cf. *Elseya/Emydura* form 1		cf. *Elseya/Emydura* form 2	
	P9215-1 holotype	P9464-157	P9464-156	P87113-45	P87103-48	P907-44 / -45	P87103-47	P895-68
L	21.3	24.4		24.1	48.2	48.8	46.5	45.3
W	24.1	**29.6**		22.5	54.8	*55.0*	38.0	**40.2**
L/W	0.88	0.82		1.07	0.88	0.89	1.22	1.13

Number of assigned individuals	8
Number of unassigned specimens	2
Minimum number of individuals	10

short-necked species is present in the assemblage.

P87108-47 and P895-68, assigned to cf. *Elseya/Emydura* form 2, are longer than wide, and the intergular extends posteriorly about half way. The pectorals are respresented posteriorly. These two specimens have proportions that conform most closely to epiplastra P923-9 and P87113-48.

Hyoplastra. The Bullock Creek sample can be sorted into four forms primarily on the basis of a suite of measurements (Fig. 19, Table 6): *Birlimarr gaffneyi*; a cf. *Birlimarr* form; and *Chelidae* forms 1 and 2. Ratios of hyoplastral length to width show some overlap between forms, but the proportions of the negative space occupied by the entoplastron show stronger differentiation.

P9464-149 and P944-10 can be referred to *Birlimarr gaffneyi.* Both are of the right size to represent mature individuals and have the humeral-pectoral groove intersecting the ento-hyoplastral suture, as in the type. P87103-50 is similar, but has slightly higher length to width ratios than specimens of *Birlimarr gaffneyi*, and the humeral-pectoral groove is confined entirely to the hyoplastron, i.e. crosses the interhyoplastral suture posterior to the entoplastron. This morphology conforms to entoplastron P87113-45, and for similar reasons to those given above for P87113-45, is assigned to a cf. *Birlimarr* form.

On the basis of entoplastral and epiplastral scute patterns (Figs 21, 23), it was anticipated that most hyoplastra in the assemblage would show some trace of the humeral scute, either due to the humeral-pectoral groove crossing the hyo-epiplastral suture, or it crossing the ento-hyoplastral suture. No part of the pectoral is present on any of the specimens of Chelidae forms 1 and 2, excepting P87112-34, in which it crosses the ento-hyoplastral suture near the level of the posterior margin of the entoplastron. Specimens in which the scute contact crosses the epi-hyplastral suture might be referrable to a *Chelodina* form, but this is not necessarily a diagnostic character of the genus, appearing to be somewhat variable (Fig. 22A). Hyoplastral morphology has not been shown or found by us to be useful in differentiating natural groups of Chelidae, and consequently the specimens not referrable to *Birlimarr gaffneyi* and cf. *Birlimarr* form can only be classified as Chelidae forms 1 and 2.

Hypoplastra. Three forms of hypoplastra are recognised: *Birlimarr gaffneyi*, gen. aff. *Elseya/Emydura* sp. indet., and Chelidae form 1 (Figs 17, 24; Table 7).

Birlimarr gaffneyi is distinguished by its small size and prounced lateral bulge of the femoral area. The larger hypoplastra group into two forms, gen. aff. *Elseya/Emydura* sp. indet and Chelidae form 1, on the basis of whether the posterior lobe tapers immediately posterior to the bridge, or whether it is parallel/sub-parallel proximally. The length to width ratios of the two forms overlap, but there is a very weak indication that form 2 is, on average, proportionally shorter than form 1. No other discrete morphological character could be found in support of the distinction though.

As already mentioned above in Systematics, P895-67 and associated carapacial fragment P895-66 may represent the same individual. P895-67 has hypoplastral morphology designated Chelidae form 1, while P895-66 is referred to gen. aff. *Elseya/Emydura* sp. indet., on the basis of its similarity to the reference specimen of that taxon (P9464-134). One obvious possibility is that gen. aff. *Elseya/Emydura* sp. indet. is dimorphic, but the apparent paradox cannot be resolved with the available material.

Xiphiplastra. Only three forms of xiphiplastra can be distinguished: *Birlimarr gaffneyi*, and Chelidae forms 1 and 2 (Fig. 25, Table 8). *Birlimarr gaffneyi* is distinguished by its small size, posterior curvature at the lateral extremity of the pubo-plastral suture, broadly oval ischio-plastral suture, and strong lateral flaring of the femoral scute region.

Chelidae form 1 is also small, but lacks a prominent femoral bulge, has no posterior curvature at the lateral extremity of the pubo-plastral suture, and the ischio-plastral suture is subtriangular. Additionally, the Chelidae form 1 xiphiplastron is thick for its size, i.e. more robust than *Birlimarr gaffneyi*, and the posterior extremity is very acute. The sutural pattern shows some resemblances to *Chelodina* species (Fig. 22), especially *C. novaeguineae*, but whether this is of systematic value is not known to us.

All the determinable large xiphiplastra are grouped in Chelidae form 2, and while there is a diversity of form in the sample, no consistency could be found in the expression of any characters or combinations of characters that supported splitting them into sub-groups. A femoral bulge, where present, is only weakly expressed. The ischio-plastral suture is oval, but in no specimens as broadly so as in *Birlimarr gaffneyi*, and the pubo-plastral suture is recurved posteriorly at the lateral extremity. The reference specimen of gen. aff. *Elseya/Emydura* sp. indet., P9464-134, has this form (Fig. 18).

Xiphiplastral morphology has not been shown or found by us from our very limited sample of comparative material to be useful in differentiating genera (or generic groups) of Chelidae, and consequently the specimens not referrable to *Birlimarr gaffneyi* can only be classified as Chelidae forms 1 and 2.

Costal 1. Four forms of costal 1 are present in the assemblage: *Birlimarr gaffneyi*, gen. aff. *Elseya/Emydura* sp. indet., a Chelidae form, and a *Chelodina* form (Fig. 26, Table 9).

In *Birlimarr gaffneyi* and gen. aff *Elseya/Emydura* sp. indet., the bridge carapace suture (BCS) on the internal surface is a broad, well-defined area, as already described above (Figs 7, 16, 17). The two can be distinguished primarily by their significant size difference.

The other two forms are distinguished by a bridge-carapace sutural area which is

Table 6. Hyoplastra – measurements and classification. Measurements in italics are estimates.

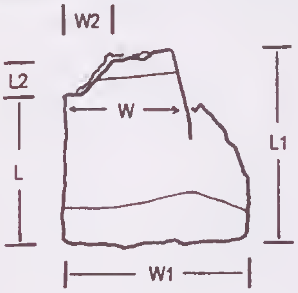
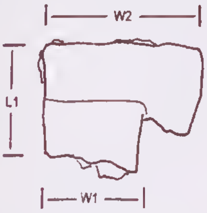
	*Birlimarr gaffneyi* gen. et sp. nov.				cf. *Birlimarr* form	Chelidae form 1					Chelidae form 2		
	L	R	L	R	R	R	R	L	L	L	L	L	L
	P9215-1 holotype		P9464-149	P944-10	P87103-50	P895-82	P895-84	P8695-129	P908-51	P87112-34	P895-85	P907-31	P895-83
L	37.3	35.6	42		51.2	54.0	*43.7*	74.0	24		29.6	30.2	47.5
L1	50.3	49.5	49.5	*53.0*	*59.3*	73.8	68.8	98.0	*35.6*		*43.8*	43.9	
W	33.1	33.6	32	37.3	*36.0*	51.2	53.1	65.2	26	53	32.9	35.9	45.7
W1	52.1	51.6					76.9				54.7		
L/W	1.13	1.06	1.32		1.42	1.05	0.82	1.13	0.90		0.90	0.84	1.04
L/W1	0.72	0.69					0.57				0.54		
L1/W	1.52	1.47	1.56	1.42	1.65	1.44	1.30	1.50	1.35		1.33	1.22	
L2	8.3	*8.6*	9.3	10.0	13.6	19.6	28.3	29.6	*9.3*	19.2	18.9	19.0	20.1
W2	11.4	12.8	12.1	15.0	18.5	22.0	29.0	28.4	8.5	19.6	10.6	14.4	15.2
L2/W2	0.73	0.67	0.77	0.67	0.74	0.89	0.98	1.04	1.09	0.98	1.78	1.32	1.32
Number of assigned individuals													12
Number of unassigned specimens													6
Minimum number of individuals													18

Table 7. Hypoplastra – measurements and classification. Measurements in italics are estimates.

	*Birlimarr gaffneyi* gen. et sp. nov.				gen. aff. *Elseya/Emydura* sp. indet.						Chelidae form 1			
	L	R	R	R	L	R	R	L	L	L	L	R	R	R
	P9215-1 holotype		P9464-166	P925-5	P9464-156 reference		P9464-155	P923-8	P87106-17 + P925-6 + P8692-23		P895-66	P895-81	P87112-33	P87103-46
L1	36.2	*38.2*	32.8	41.5	96.4	82.3	*105.6*	60.9		*65.3*	93.6	32.0	46.5	100.2
W1	30.7	30.6	26.4	35.4	76	77.9	84.3	52.8	79.2	*55.3*	90.7	35.2	40	90.4
W2	52.4	51.8						87.3	128.4		152.2			
L1/W1	1.18	1.25	1.24	1.17	1.27	1.06	1.25	1.15		1.18	1.03	0.91	1.16	1.11
L1/W2	0.69	0.74						0.70			0.61			
W1/W2	0.59	0.59						0.60	0.62		0.60			
Number of assigned individuals														12
Number of unassigned specimens														9
Minimum number of individuals														21

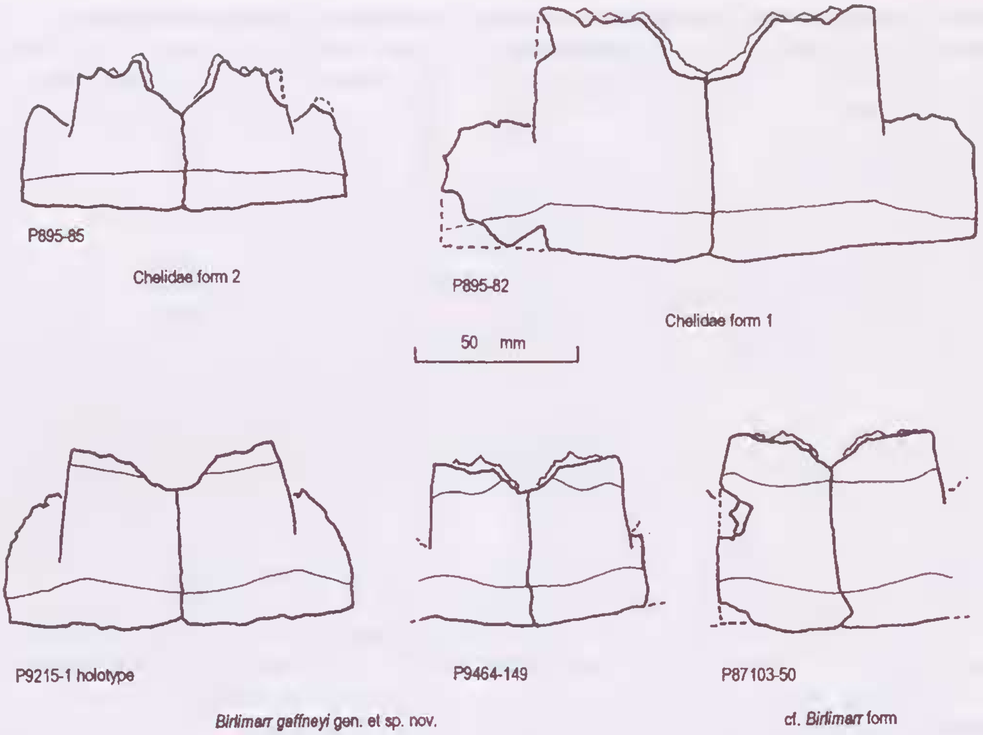


Fig. 24. Hyoplastra. Excepting P9215-1 (*Birlimarr gaffneyi* gen. et sp. nov.), each of the specimens is mirrored.

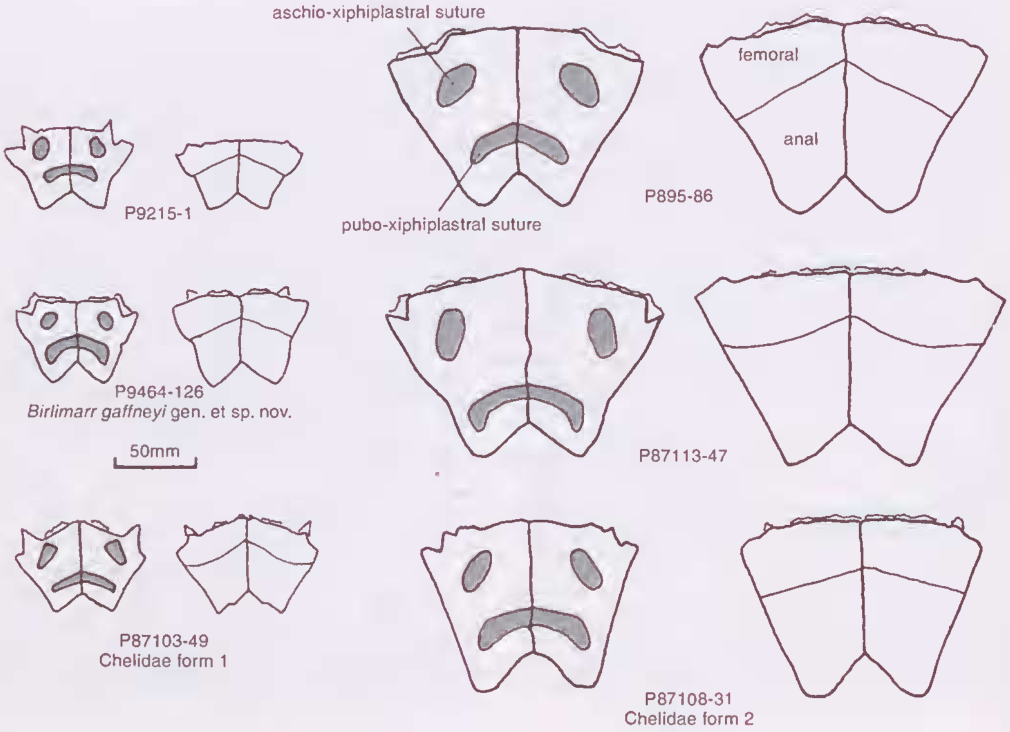


Fig. 25. Xiphiplastra. Excepting *Birlimarr gaffneyi* gen. et sp. nov., P9215-1, each of the other specimens is mirrored.

widest medially and narrows laterally to almost just a thin ridge. This morphology is apparently diagnostic of *Emydura* amongst short-necked chelids (Thomson *et al*. 1997), but is similar in long-necked *Chelodina* (Fig. 27). Additionally, in *Chelodina* the bridge carapace suture appears to be imposed right across the trace of the rib, whereas in *Emydura* and in short-necked species in general, it is imposed on the rib (see Thomson *et al*. 1997), rather than across it. P87115-33 is noteworthy in that the bridge carapace suture clearly extended onto costal 2, which has been observed by us to occur in *Chelodina novaeguineae* and *C. longicollis*: there is some individual variability in this feature, sometimes the bridge carapace suture stops just short of the pleural 1-2 suture, but the superimposition of the BCS over the rib is retained. Thus P87115-33 is assigned to a cf. *Chelodina* form. P908-49 has a similar BCS morphology, but it stops well short of the pleural 1-2 suture, and its cross-cutting relationship to the rib is not so strongly expressed. It may represent another *Chelodina*-like form or an *Emydura*-like form, but insufficient data are available to make a generic determination, and consequently it is simply assigned to a Chelidae form.

Nuchals. All nuchals in the Bullock Creek sample have a cervical scute. Only four informative isolated examples are present in the analysed sample, in addition to that of the *Birlimarr gaffneyi* type (Fig. 6) and those of gen. aff. *Emydura/Elseya* sp. indet. shown in Figures 15 and 16, and are referred to these taxa (Table 10).

Costal 8. Costal 8 is readily identifiable amongst costals as it usually bears the bulk of the carapacial-ilial sutural contact. In extant chelids examined, the sutural contact variously extends posteriorly onto the suprapygal and/or anteriorly onto costal 7. Four forms of costal 8 are present in the Bullock Creek LF assemblage: *Birlimarr gaffneyi*; gen. aff. *Elseya/Emydura* sp. indet., a Chelidae form; and a *Chelodina* form (Fig 28, Table 11).

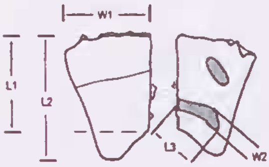
The *Birlimarr gaffneyi* is distinguished by its small size, and weak expression of the ilial-carapacial suture, which just extends onto the suprapygal and just onto costal 7. On the dorsal surface, the contact between the vertebral 4 and pleural 4 scute runs parallel to the posterior margin. The costal 8 of gen. aff. *Elseya /Emydura* sp. indet. is larger, and the ilial-carapacial suture better defined and more extensive on costal 7, but the scute pattern and length to width proportions are similar. The Chelidae form is proportionally short, the ilial-carapacial suture very strongly defined (considerably more so than in gen. aff. *Elseya /Emydura* sp. indet.) and fails to cross the costal 7-8 suture, but does extend onto the suprapygal. In the Chelidae form, contact of the vertebral 4 and pleural 4 scutes crosses the costal 8-suprapygal suture medially.

In P895-92 and P894-13, the ilial-carapacial suture is extensive on costal 7 but does not extend posteriorly onto the suprapygal. From specimen P894-13, it is clear that the suprapygal was quite a small bone. The morphology of P894-13 has similarities to extant *Chelodina rugosa*, which has a diminutive suprapygal that bears no part of the ilial-carapacial suture (Fig. 28C). The costal 8 of P894-13 is not as expanded at the expense of the suprapygal as in *Chelodina rugosa*. *Chelodina longicollis* and *C. novaeguineae* both have proportionally large suprapygals with ilial contact, similar to those of Emydurodds examined. P894-13 and P895-92 are assigned to a *Chelodina* form on the basis of their similarities to *Chelodina rugosa*.

Suprapygal. Three forms of suprapygal can be discriminated with certainty, but there may be a fourth amongst the small sample of suprapygals available, and a fifth form can be inferred from the morphology of costal 8 specimen P894-13 (designated a *Chelodina* form) as already described above. The suprapygal of the gen aff. *Elseya/Emydura* sp. indet. reference specimen (P9464-134, Figs 15, 28) is unfortunately damaged. The indications are that the length to width ratio was probably low (Fig. 15C), more like in *Birlimarr gaffneyi* (Figs 5, 28) than in the otherwise similar larger specimens assigned to Chelidae form 1 (Fig. 29, Table 12).

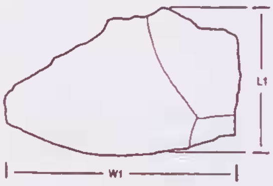
Birlimarr gaffneyi is characterised by: its small size; a width almost double the length;

Table 8. Xiphiplastra – measurements and classification. Measurements in italics are estimates. P87115-37 is determinate, but not measurable in the scheme used.



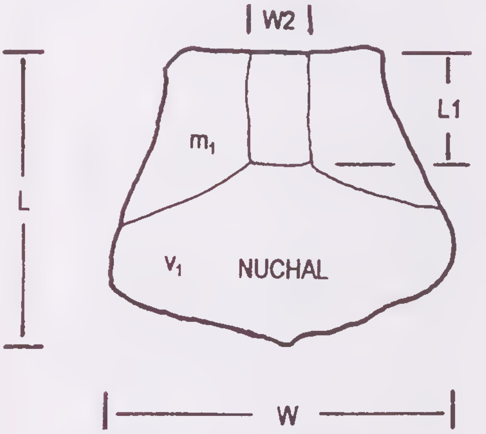
	Birlimarr gaffne gen. et sp. nov			Chelidae form 1			Chelidae form 2							(gen. aff. *Elseya/Emydur.* sp. indet.)	
	L	R	R	R	R	L	R	R	L	R	R	R	R	L	R
	P9215-1 holotype		P9464-126	P87103-49	P908-50	P87115-37	P87113-47	P8695-147	P895-86	P87108-31	P8695-156	P87108-33	P907-38	P9464-134 reference	
L1	*29.3*	*29.3*	29.0	31.8			68.2	60.9	70.1	60.7	*58.0*	*58.2*			
L2	37.5	37.3	39.2	37.5			83.6	78.0	81.9	77.0	75.6				
L3	9.9	10.0	10.3	11.6	12.4		24.8	22.7	23.0	18.5	23.4	23.0	27.1		20.5
W1	*30.2*	*30.2*	*30.3*	29.0	32.4		68.3	56.6	60.6	52.6	*61.2*			66.9	75.5
W2	5.8	5.7	6.2	6.4	6.0		12.7	11.4	11.3	9.3	11.5	11.4	13.3		8.8
L1/W1	0.97	0.97	0.96	1.10			1.00	1.08	1.16	1.15	0.95				
L2/W1	1.24	1.24	1.29	1.29			1.22	1.38	1.35	1.46	1.24				
L3/W3	1.71	1.75	1.66	1.81	2.07		1.95	1.99	2.04	1.99	2.03	2.02	2.04		2.33
Number of assigned individuals															13
Number of unassigned specimens															18
Minimum number of individuals															31

Table 9. Coastal 1 – measurements and classification.



	Birlimarr gaffneyi gen. et sp. nov.								gen aff. *Elseya/Emydura* sp. indet.			*Chelodina* form cf. *C. novaeguineae*		Chelidae form		
	L	R	R	R	R	R	R	R	L	R	L	L	L	R	L	R	R
	P9215-1 holotype		P87105-17	P9464-137	P9464-139	P9464-140	P9464-142	P9464-138	P9276-6	P9464-134 reference	P895-67	P923-7	P87115-33	P8692-24	P908-48	P895-94	P895-94
L1	29.3	29.7	34.4	30.6	32.3	28.3				76.5	*86.2*	*79.3*		36.8	42.4	46.4	46.4
W1	48.7	48.8	59.4	53.6						122	135.3	119.6		60	68.4		
L1/W1	0.60	0.61	0.58	0.57						0.63	0.64	0.66		0.61	0.62		
Number of assigned specimens																	15
Number of unassigned specimens																	8
Minumum number of individuals																	23

Table 10. Nuchals – measurements and classification. Measurements in italics are estimates; bold = 2 x half width.



	Birlimarr gaffneyi gen. et sp. nov.			gen. aff. *Elseya/Emydura* sp. indet.			
	P9215-1 holotype	P9464-135	P9464-148	P9464-134 reference	P895-67	P895-80	P9464-134
L	*29.3*	29.5	*27.0*	68.4	*73.7*	55.1	63.8
W	**34.4**	35.8	***33.0***	**79.8**	82.0	**61.2**	70.3
L/W	0.85	0.82	0.82	0.86	0.90	0.90	0.91
L1	11.2	12.10	11.40	36.00	36.80	25.00	25.9
W1	**6.8**	6.0	3.9	19.7	9.8	9.7	6.3
L1/W1	1.65	2.02	2.92	1.83	3.76	2.58	4.11
L1/L	0.38	0.20	0.42	0.53	0.50	0.45	0.41

proportionally wide pygal-suprapygal contact; complete coverage by the vertebral 5 scute; and by a weakly defined sutural contact with the ilium. In contrast, Chelidae form 1 has a length to width ratio in the order of 3:4, the pygal-suprapygal contact is proportionally narrow, and the ilial sutural surface is well defined. Coverage by the vertebral 5 scute in Chelidae form 1 is complete.

P8695-130 and P925-2 are intermediate in length to width ratio and have well defined ilial sutural surfaces and narrow pygal-suprapygal contact. Unlike in any of the other forms of suprapygal, the fourth pleural scale covered the bones laterally. The two specimens are designated Chelidae form 2.

ANALYSIS OF THE ASSEMBLAGE

Estimated minimum number of species. Three nominal forms and one species are diagnosed above: gen. aff. *Elseya/Emydura* sp. indet., *Chelodina* sp. A and *Chelodina* sp. B; and *Birlimarr gaffneyi* From the forms of entoplastra, two additional short-necked species are indicated, though one less certainly than the other.

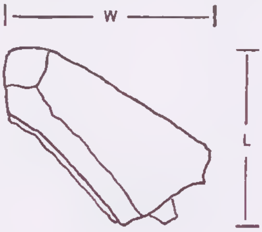
Amongst the sample of Bullock Creek LF entoplastra, no *Chelodina* are indicated, but four short-necked forms are recognisable. Only one of these forms is diagnosable (*Birlimarr gaffneyi*). Parsimony dictates that one or the other of the two large *Elseya/Emydura* forms most probably represents gen. aff. *Elseya/Emydura* sp. indet. Thus, one additional large species of *Elseya/Emydura* can be postulated, and added to the total of diagnosed species. The cf. *Birlimarr* form may represent an additional species, but this is somewhat less certain because it is just possible that the entoplastron assigned to the form (and possibly the hyoplastron which conforms to it) could represent sub-adults of one or the other of the two large *Elseya/Emydura* species.

A variety of individual bones of the turtle shell seem to offer a practical means of determining species diversity in fossil assemblages in which relatively intact specimens are the exception. The methodology applied here, however, warrants further testing by more comprehensive analogy with extant chelid species.

In summary, there is evidence for five, and possibly six species of chelid in the Bullock Creek LF, though only four forms are sufficiently represented at present to assign to a taxonomic group below the level of infrafamily.

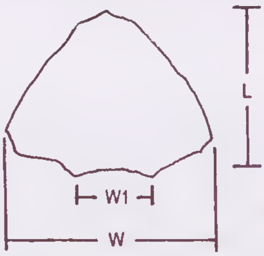
Estimated minimum number of individuals. The highest minimum number of individuals indicated by any individual bone is 31 (xiphiplastra: Table 7). However, the minimum number of individuals in the whole assemblage is considerably higher. Other plastral elements not in sutural contact

Table 11. Costal 8s – measurements and classification. Measurements in italics are estimates.



	Birlimarr gaffneyi gen. et sp. nov.			gen. aff. *Elseya/Emydura* sp. indet.			Chelidae form	*Chelodina* form	
	R	R	L	R	L	R	L	R	R
	P9215-1 holotype	P87113-50	P87103-53	P9464-134 reference		P927-4	P8694-10	P894-13	P895-92
L	24.0	26.9	32.7	63.8	59.3	59.8	30.2		29.7
W	28.4	*29.5*	35.7	66.7	72.0	70.1	48.6		*37.0*
L/W	0.85	0.91	0.92	0.96	0.83	0.85	0.62		0.80
Ilial carapacial suture well-defined	N	N	N	Y	Y	Y	Y	Y	Y
Ilial carapacial suture extends onto costal 7	Y	Y	Y	Y	Y	Y	N	Y	Y
Ilial carapacial suture extends onto suprapygal	Y	Y	Y	Y	Y	Y	Y	N	N

Table 12. Suprapygals – measurements and classification. Measurements in italics are estimates; bold = 2 x half width.



	Birlimarr gaffneyi gen. et sp. nov.	gen. aff. *Elseya/Emydura* sp. indet.	Chelidae form 1 ? = gen aff. *Elseya/Emydura* sp. indet.			Chelidae form 2	
	P9215-1 holotype	P9464-134 reference	P9612-3	P925-3	P87103-59	P8695-130	P925-2
L	17.3	49.0	48.2	24.9	39.5	30.2	34.0
W	**31.0**		59.4	**34.4**	**48.8**	47.9	50.0
L/W	0.56		0.81	0.72	0.81	0.63	0.68
W1	13.9		22.5	12.5	17.2	18.6	18.4
W1/W	0.49		0.38	0.36	0.35	0.38	0.37
Pleural scutes present	N	N	N	N	N	Y	Y
Ilial insertion well defined	N	Y	Y	Y	Y	Y	Y

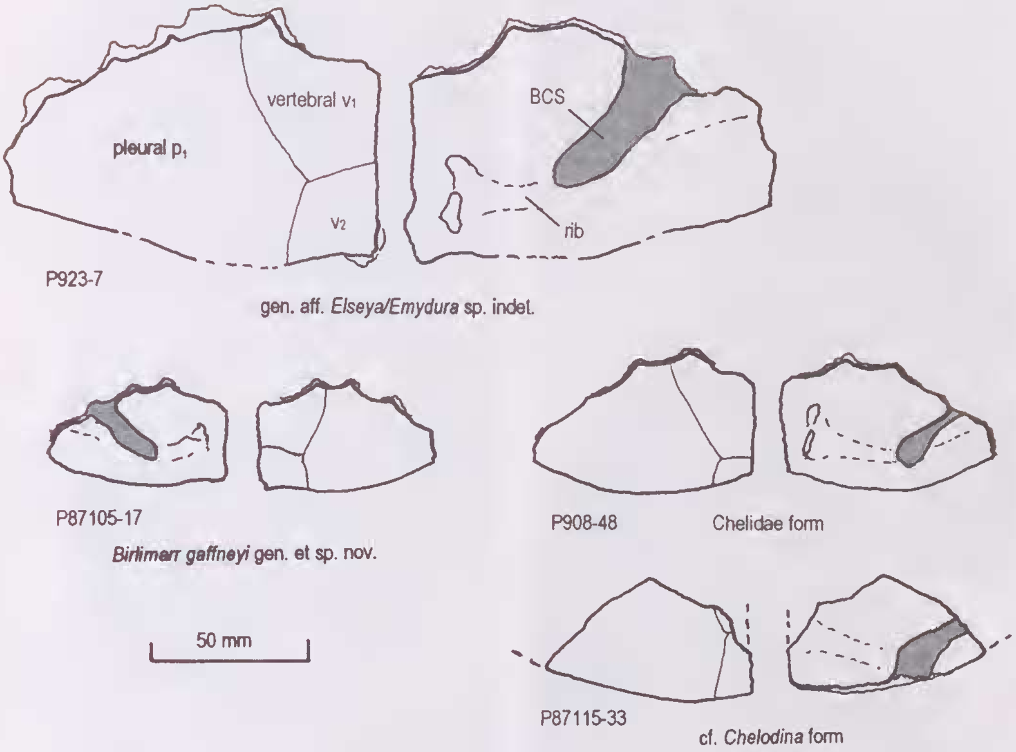


Fig. 26. Costal 1. The costal 1 of gen. aff. *Elseya/Emydura* sp. indet. reference specimen (P9464-134) and referred specimen (P895-67) are shown in Figures 16 and 17 and that of the *Birlimarr gaffneyi* gen. et sp. nov. holotype (P9215-1) in Figure 7.

with each other can be progressively be added to the xiphiplastral total in the anatomical order xiphiplastra > hypoplastra > hyoplastra > epiplastra + entoplastra. (Theoretically, one could continue onto the carapace.) This method may result in an overestimate for the assemblage, as, for example, an isolated xiphiplastron may represent the same individual as an isolated hyoplastron. A more rigorous comparison of the relative size of each element not in sutural contact in the skeleton could be used to identify and take into account all such possibilities. However, the effort involved at arriving at a reasonable estimate of the minimum number of individuals in the sample is not justified. Very few individuals are represented by specimens consisting of two or more bones (only P9215-1, P9464-134, P9564-155 and P895-67). Only P9464-155 was completely re-sutured after preparation, and then from bones whose close association had been noted during preparation: the others were prepared with at least some of their bones in sutural contact. Chelids in the assemblage are therefore typically completely disarticulated and their elements widely dispersed at the scale at which the deposit has been sampled by quarrying. Three of these individuals are represented by at least one xiphiplastron and one hypoplastron, and there are several xiphiplastra and one hypoplastron (P895-66) of the right size to represent the carapacial fragment P895-67 individual. In order to ensure that these individuals or possible individuals are only counted once, four individuals are discounted for every plastral bone besides the xiphiplastron.

Using the estimation method outlined above, and bearing in mind that part of the methodology for this study involved testing

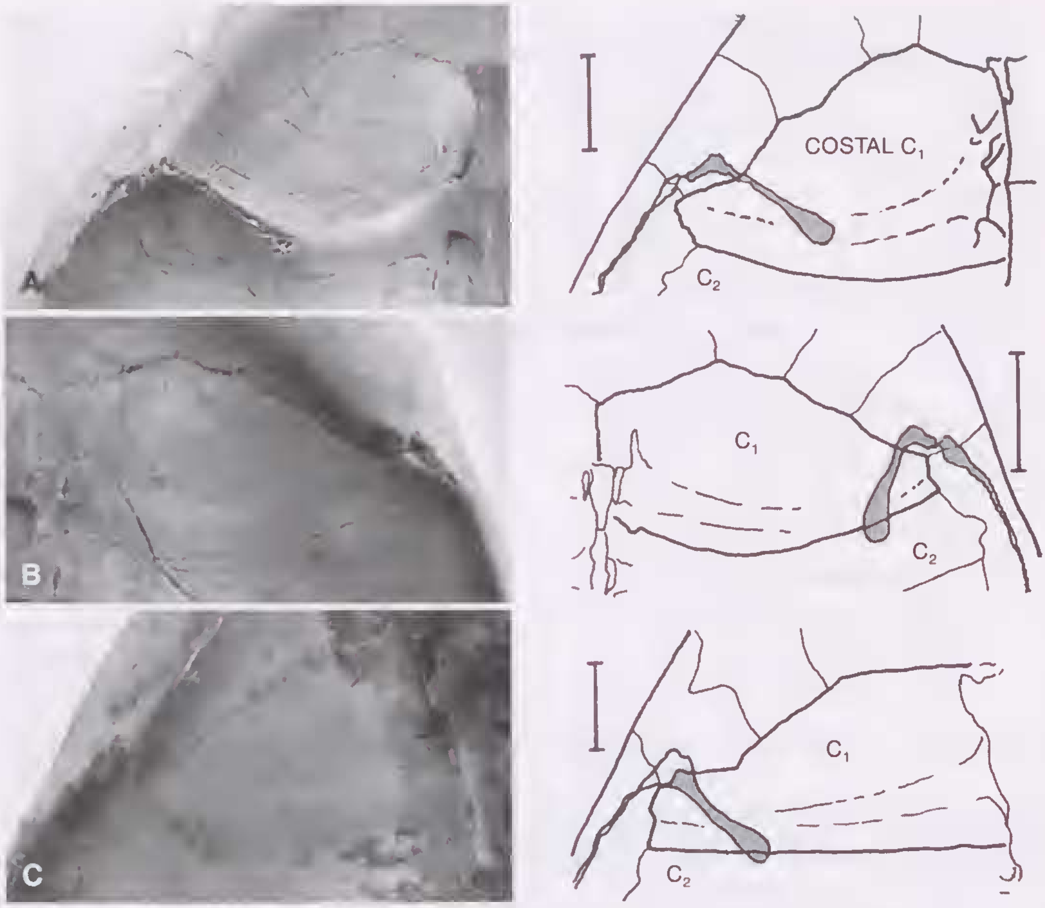


Fig. 27. Internal morphology, showing the shape and extent of the bridge carapace suture (BCS) on costal 1 in: **A**, *Chelodina rugosa* (unregistered carapace); **B**, *C. longicollis* (NTM R.24812); **C**, *C. novaguineae* (NTM R.16325). Scale bars = 20 mm.

each bone against every other bone it could possibly be sutured to, the analysed Bullock Creek chelid assemblage can minimally be accounted for by 77 individuals. [Xiphiplastra (31) + hypoplastra (21-4) + hyoplastra (18-4) + epiplastra (13-4) + entoplastra (10-4) = 77].

Most of the determined material appears to belong to species of Emydurodd. Establishing the frequency of Chelodd (*Chelodina*) is problematic because much of the material could not be classified to infrafamily or lower level. Out of ten individuals classified by epiplastra, four are *Chelodina*. The only other material identified as possibly representing *Chelodina* is one xiphiplastron and two costal 8s. A frequency of about 9% (7 out 77 individuals) of Chelodd in the assemblage is suggested as a first order approximation.

Evidence of predation by crocodiles. As remarked above, chelids in the Bullock Creek LF assemblage are typically completely disarticulated and their elements widely dispersed. The exceptional preservation of P9215-1 warranted special attention to its taphonomy, and it was concluded above in the description of *Birlimarr gaffneyi* that the holotype was the victim of a crocodile. What is exceptional about the holotype of *Birlimarr gaffneyi* is not the evidence for crocodile attack, but its completeness.

The role of crocodilians in the accumulation of the Bullock Creek Local

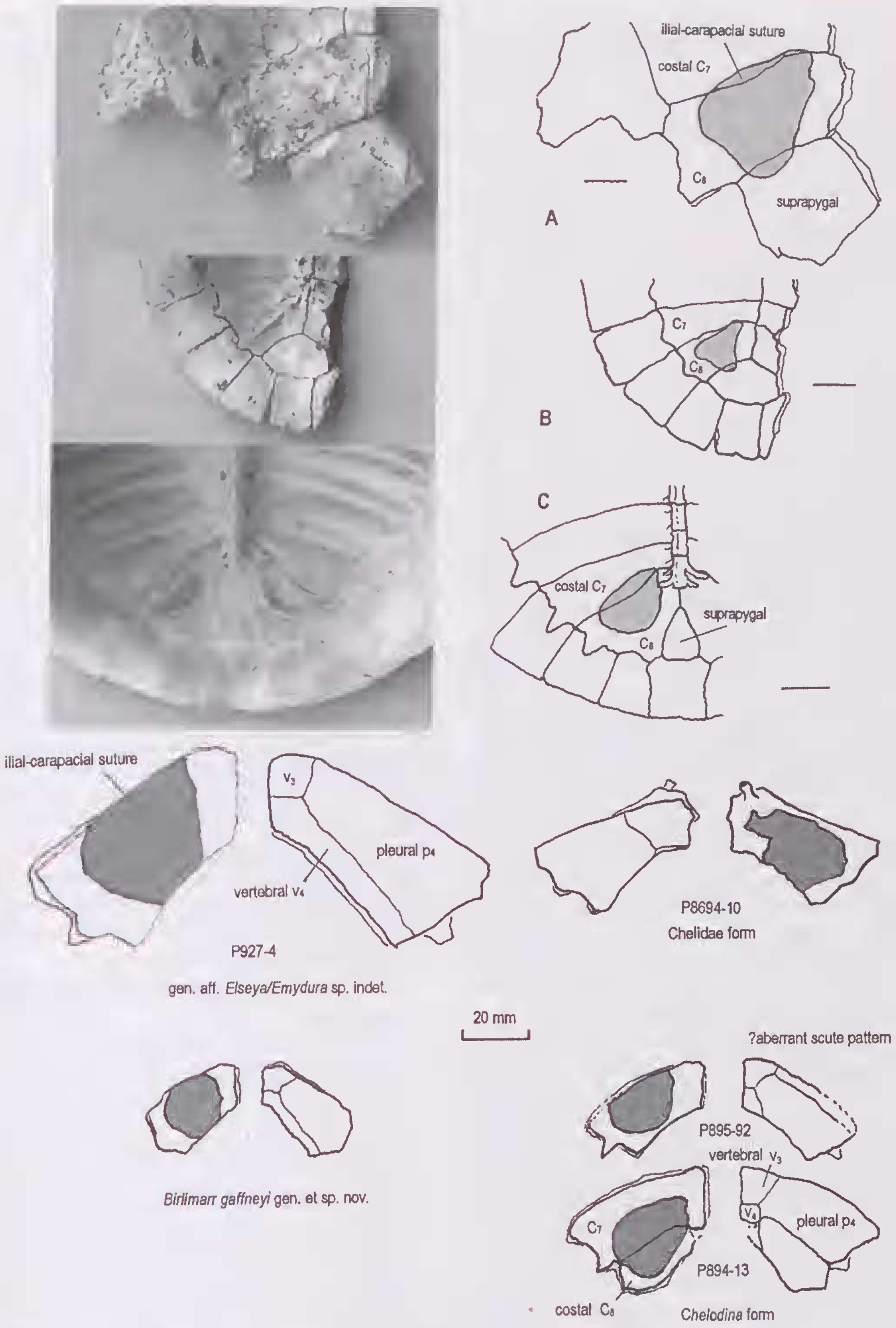


Fig. 28. Costal 8. Relationships of ilial-carapacial suture to bone of the carapace in: **A**, gen. aff. *Elseya/Emydura* sp. indet. reference specimen P9464-134; **B**, *Birlimarr gaffneyi* gen. et sp. nov. holotype P9215-1; and **C**, extant *Chelodina rugosa*, R.24813. Scale bars 20 mm.

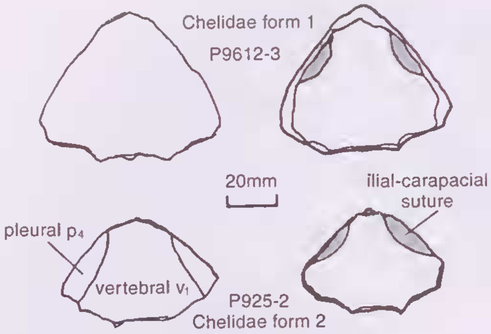


Fig. 29. Suprapygals, Chelidae form 1 and form 2.

Fauna was alluded to by Murray and Megirian (1992). Murray (1986) drew attention to tooth puncture marks in the holotype of the marsupial tapir *Propalorchestes novaculacephalus*, but the NTM Bullock Creek LF assemblage contains numerous taxa that can be identified as crocodile victims. Work in progress on this aspect of the assemblage will be more fully reported elsewhere.

Several examples of crocodilian predator damage to chelid shells are shown in Figure 30. They include depressed areas, sometimes with distinct point impacts, with radiating irregular fractures. Clean punctures such as have been found in avian limb bones for example, are uncommon, possibly due to the flexibility of the spongy bone of turtle shells. Many isolated chelid shell bones preserve this evidence, the fractured bone often having remained together, presumably due to the cohesive properties of collagen and soft tissues, though bones of the shell became disarticulated and separated from each other before burial. Numerous highly fractured turtle bones survive acid-processing, which appears to be due to the presence of early diagenetic crystalline calcite (as fringing cements) in the fractures. Crystalline calcite is slightly more resistant to acid digestion, compared to the micritic matrix typical of the fossiliferous facies, presumably due to lower free surface energy of the larger crystal faces. The hardening agent used in preparation (Synacryl 9122X) progressively replaces the calcite cement, thereby maintaining the relationships of fragments. Ten out of the 21 individuals represented by hypoplastra, for example, exhibit fracturing characteristic of predator damage: all the others are either perfectly intact, or else have planar to curviplanar broken surfaces that are attributable to post-depositional breakage or quarrying of the host limestone. A similar pattern is evident on all the other bones listed above, and suggests that most individuals in the assemblage were preyed upon or scavenged by crocodilians.

Palaeoecology. The present aquatic turtle diversity of Australian river systems is low compared to that of other continents (Gaffney 1991), and occurrences of more than four sympatric species are notable. Georges and Adams (1996) record that the Douglas-Daly River system of the Northern Teritory contains eight turtle species (seven chelids plus the Pig-nosed Turtle, *Carrettochelys insculpta* (Carrettochelydidae), which is more than have been recorded in any other river system, but so far only six species (five chelids plus *Carrettochelys*) have been observed in sympatry. White (1997) reports five sympatric chelid species in the Gregory River (Queensland) at Riversleigh. Amongst climatic variables, total annual precipitation (but not the seasonal distribution of this rainfall), mean annual temperature, and frost-free days, in that order, appear to be the major factors controlling turtle diversity on Australia today (Pianka and Schall 1981), to which may be added the physiographic factor of habitat variation.

The two river systems with the highest recorded turtle diversity in Australia today are in a zone where mean annual temperature is in the order of 27°C, there are no frost days, and median annual precipitation within the catchments varies from about 500 mm inland to about 1200 mm in coastal areas for the Douglas-Daly system and from about 400 mm inland and about 800 mm at the coast for the Gregory system. This rainfall is highly seasonal in its distribution, with most falling during the summer wet season (Bureau of Meterology 1989). Significant flow in both these river systems is maintained throughout the year by groundwater discharge, in contrast to many other rivers in the region which flow only seasonally, and perennial bodies of water become limited to billabongs.

The presence of five and possibly six species in the Miocene Bullock Creek Local Fauna is comparable to the six species of chelids reported from Miocene Carl Creek Limestone, Queensland, assemblages by White (1997), and suggests that comparatively low turtle diversity in Australian freshwater systems is a long established pattern. By analogy with present day patterns of chelid species diversity, palaeoenvironmental conditions at both Miocene fossil localities appear to have been in the optimal range for chelids. In both Miocene assemblages, the chelid fauna is dominated by Emydurodd species, with *Chelodina* (Chelodd) a minor component. The presence of pseudemydurines in the Carl Creek Limestone suggests that some ephemeral swamp habitats such as those occupied by the extant species, *Pseudemydura umbrina*, may have been present at Riversleigh. As for the Carl Creek Limestone assemblages, the high frequency of Emydurodd species and low frequency of carnivorous *Chelodina* in the Bullock Creek LF implies the presence of clear, perennial water bodies with an aquatic flora suiting the omnivorous diets of most emydurodds (White 1997). Ephemeral and perennial aquatic depositional environments with the general characteristics inferred above have been recognised from sedimentological data in the Carl Creek Limestone (Megirian 1992, 1997, in prep.) and in the Camfield Beds (Murray and Megirian 1992).

PHYLOGENY RECONSTRUCTION

Introductory remarks. Gaffney's (1977) phylogeny of chelids, based on osteological characters, provides the basic foundation for evaluating the possible phylogenetic affinities of *Birlimarr gaffneyi*. By way of a preliminary analysis, *Birlimarr gaffneyi* was scored for the informative subset of characters by which Gaffney diagnosed chelid clades and processed using techniques available in Phylip (Felsenstein 1986) and Hennig86 (Farris 1988). As expected, *Birlimarr gaffneyi* was resolved as a member of Gaffney's Chelinae. In terms of phenetic similarities to *Emydura, Elseya, Rheodytes* and *Elusor* (Tables 1-3), *Birlimarr gaffneyi* is a member of Gaffney's (1977) Emydurodd, a taxon which has not been diagnosed by shared derived characters.

Thomson *et al.* (1997) nominated five post-cranial osteological characters, including a novel one of the morphology of the bridge carapace suture on costal 1, as useful in diagnosing Australian short-necked chelid turtles to genus/generic group level. The objective of Thomson *et al.* (1977) was not phylogeny reconstruction, and consequently their expressed or implied character polarities were not discussed in any detail or substantiated by reference to an outgroup to the Chelidae. Polarity was specified for their characters A, C and E, but not explicitly for B and D. The phylogenetic analysis of these and other characters is the subject of work in progress by S. Thomson (written comm. February, 1999), using South American chelids and *Pelomedusa* as outgroups. *Birlimarr gaffneyi* was added to the matrix, which was then analysed using Hennig86. The character matrix and resulting consensus trees are shown in Figure 20.

A new hypothesis of relationships between Australian chelids at generic level, which incorporates *Birlimarr*, is proposed here, based on a combination of useful morphological characters (in some cases re-defined) drawn from Gaffney (1977), Cann and Legler (1994), Thomson *et al.* (1997), as well as two additional ones suggested to us by the study of *Birlimarr gaffneyi*. By 'useful', we mean apparently derived characters shared by at least two of the ingroup basic taxa, as defined below; autapomorphic characters that merely help diagnose terminal branches are not discussed or analysed.

In discussion below of character polarities, references are made to a variety of 'pelomedusids', including the recently re-described Early Cretaceous (possibly Albian) Santana Formation (Brazil) species, *Araripemys barretoi* Price (Meylan 1996). A second early pelomedusid from the Santana

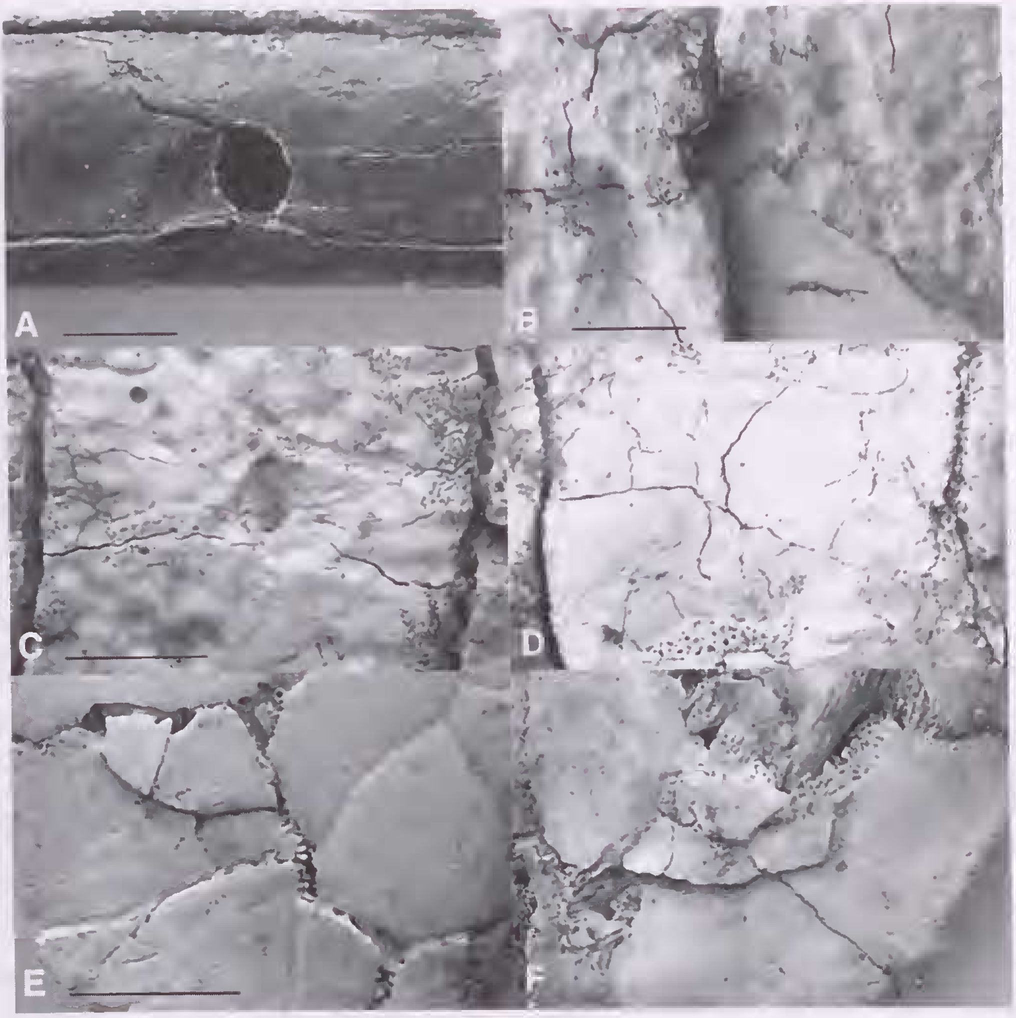


Fig. 30. Evidence of predator damage to Bullock Creek LF vertebrate remains. **A**, avian long-bone with a tooth puncture mark with cross-sectional shape characteristic of the teeth of the crocodilian *Baru darrowi*; **B** tooth puncture in turtle carapace P9464-134; **C**, external point impact and **D**, associated fractures inside turtle carapace P9464-134; **E** (external view) and **F** (internal view) of a depressed fracture thought to have been caused by a crocodilian in the plastron of the *Birlimarr gaffneyi* gen. et sp. nov. holotype P9215-1. Scale bars: 10 mm.

Formation, described by Gaffney and Meylan (1991) and included in Meylan's (1996) phylogenetic analysis has yet to be named and is referred to here by its catalogue number, SMF 4922 (= FR 4922 in Meylan, 1996). In Meylan's (1996) revised systematics, the Pelomedusidae is one of four families within the hyperfamily Pelomedusoides, but here the term 'pelomedusid' is used in the broad sense of Gaffney and Meylan (1988), rather than strictly for the living genera *Pelusios* + *Pelomedusa*. Meylan (1996) resolved *Araripemys barretoi* + SMF 4922 as a sister clade, the Araripemydidae, to all other pelomedusids. *Araripemys barretoi* appears to be quite a specialised pelomedusid in some respects, especially in shell morphology, but SMF 4922 is quite generalised and is thought to provide a fair indication of the primitive states of the outgroup.

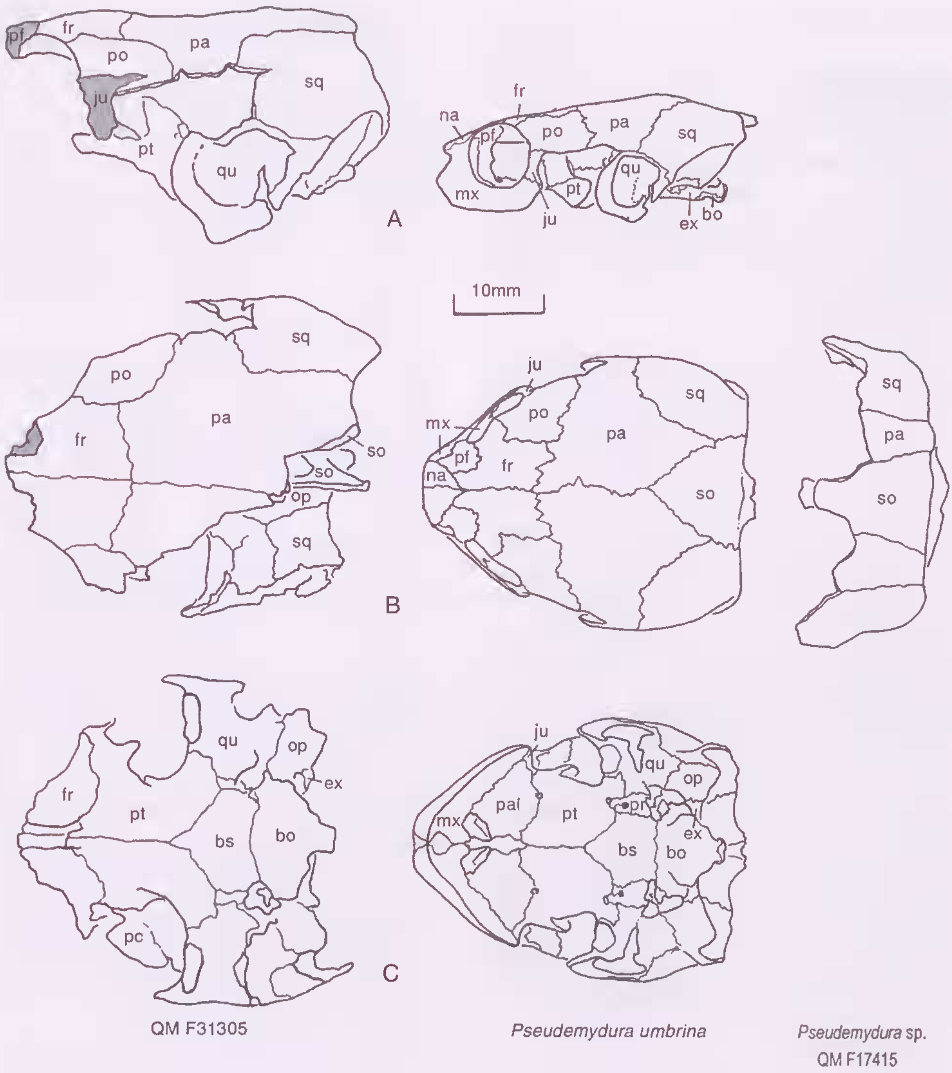


Fig. 31. Cranial structure of the pseudemydurines QM F31305 (Miocene Carl Creek Limestone – after White 1997: fig. 4), *Pseudemydura umbrina* (Recent – after Gaffney 1977: figs 1B, 2B, 4B) and *Pseudemydura* sp. QM F17415 (Miocene Carl Creek Limestone - after Gaffney *et al.* 1989: fig. 1C). **A**, lateral view (QM F31305 reversed); **B**, dorsal view; **C**, ventral view. Sutural surfaces stippled.

Basic taxa. Gaffney (1977) and Thomson *et al.* (1997) compared different sets of basic taxa, and so their matrices cannot simply be combined. The following basic taxa are used in this analysis: *Pseudemydura, Elseya latisternum* generic group (GG); *Elseya dentata* GG; *Emydura, Rheodytes*, and *Birlimarr*. The un-named chelid skull from the Miocene Carl Creek Limestone, QM F31305, described by White (1997) is also analysed (Fig. 31). *Elseya novaeguineae* and the Queensland *Elseya* species complex are simply treated here as part of the *Elseya dentata* generic group (Fig. 3), though they have some distinctive character expressions (Fig. 20). This selection facilitates comparison of our results with hypotheses of relationships presented by Gaffney (1977), Georges and Adams (1992) and Georges *et al.* (in press)

	characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
PELOMEDUSIDS	0	0	0	0	?	?	?	0	0	0	?	?	0	0	0	0	0
Pseudemydura	1	1	1	0	0	0	0	0	?	1	0	0	1	1	1	1	1
QM F31305	1	1	?	?	?	?	?	?	0	1	0	?	1	1	1	1	1
Elseya latisternum GG	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Elusor	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0
Rheodytes	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0
Birlimarr gen. nov.	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Emydura	1	1	1	1	1	3	1	0	0	1	1	0	0	0	0	0	0
Elseya dentata GG	1	1	1	1	1	2	1	0	0	1	1	0	0	0	0	0	0

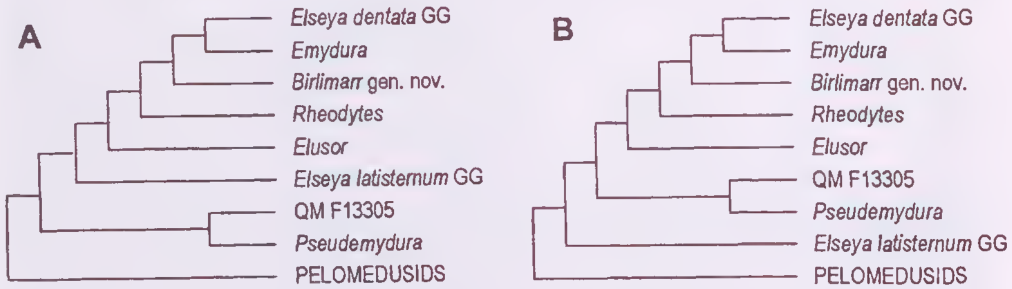


Fig. 32. Generic level hypotheses of phylogeny of Australasian short-necked chelids based on shared, derived morphological characters, analysed using Hennig86, Version 1.5 (Farris 1988). (Equally short trees; consistency index, 82; retention index, 78).

(Figs 2-4), which we regard as being the currently best resolved hypotheses of relationships. Cann and Legler (1994) analysed a combined set of characters (morphological, biochemical and behavioural) and while their results are interesting, their model is not easily tested by, or applicable to the evaluation of, hypotheses resulting from discrete sets of data.

Without an ideal set of comparative material, and without a comprehensive knowledge of chelids in particular or turtles in general, we are compelled to assume that the specimens at our disposal, and those depicted in the literature, are representative of the basic taxon to which each specimen belongs. Legler and Cann (1980) state that their observations on *Elseya dentata* and *Elseya latisternum* are true of all species in their generic groups. Wherever possible we have verified observations presented by Gaffney (1977), Thomson *et al.* (1997), Legler and Cann (1980) and Cann and Legler (1994) in our own material, and where specified, accept their polarity determinations unless as discussed below. Character states for *Rheodytes* were scored from information in Legler and Cann (1990), and for *Elusor* from Cann and Legler (1994).

Description of characters. Characters are expressed as the derived state relative to the pelomedusid outgroup, and their expression for each of the basic taxa are given with Figure 32.

1. Unusually developed lateral cheek emargination (Gaffney 1977: synapomorphy of Chelidae).
2. Loss of quadratojugal (Gaffney 1977: synapomorphy of Chelidae).
3. Loss of mesoplastra (Gaffney 1977: synapomorphy of Chelidae).
4. Anterior frontal process at least partially separating nasals (Gaffney 1977: synapomorphy of Chelinae).
5. Bridge carapace suture BCS diverges anterolaterally from trace of the rib on pleural 1 (Thomson *et al.* 1997: table 1, character A).
6. Bridge carapace suture morphology:

multistate (Thomson *et al.* 1997: table 1, character B): 0 (= state 1 of Thomson *et al.* 1997) - anterior and posterior edges diverge, widest distal to vertebral column; 1 (= state 2 of Thomson *et al.* 1997) - anterior and posterior edges essentially parallel, with prominent suture surface between them; 2 (= state 3 of Thomson *et al.* 1997) - prominent suture surface with marked medial constriction; 3 (= state 4 of Thomson *et al.* 1997) - sutural surface widest proximal to vertebral column, constricting distally to form a ridge.

7. Trace of rib on pleural 1 showing no distal posterior inflection, and no axial torsion (Thomson *et al.* 1997: table 1, character C).
8. First vertebral scute narrower than the second. Thomson *et al.* (1997: table 1, character D) identify two states of vertebral proportions: 'first three vertebral scutes equal or subequal in width' scored as 1 and 'first vertebral scute wider than the second and third' scored as 2, placing no order (polarity) on the two states (S. Thomson pers. comm.). Gaffney (1977 - corrected in Gaffney 1979a: 13) identified 'first vertebral scute (wider) than second' as a derived condition within chelids, and identified it as a synapomorphy of Chelodd. In *Pseudemydura*, the first vertebral scute is narrower than the second, but unlike in other short-necked forms, is parallel-sided (Thomson *et al.* 1997: fig. 4A), and this particular character expression is regarded here as an autapomorphy of *Pseudemydura umbrina* and scored as ? for this analysis. In the primitive pelomedusid SMF 4922 (Gaffney and Meylan 1991), the first vertebral scute is wider than the second, and this is taken here as indicative of the primitive state. (*Araripemys barretoi* is unusual in having the anterior part of the carapace emarginated so that the first vertebral scute is in a marginal position, rather than bounded anteriorly by peripherals - Meylan 1996: fig. 1). The common condition of the first vertebral scute being about equal in width to the second is also here regarded as being plesiomorphic, so that the derived condition is the state in which the first vertebral scute is distinctly narrower than the second.
9. Posteromedial process of frontal partially separating parietals. In *Birlimarr gaffneyi*, the frontal has a medial posterior projection partially separating the parietals. A similar structure is present in *Elseya latisternum*. There appears to be no such structure in *Emydura victoriae* and *Emydura macquarii*, discounting any miniscule expression in some individuals which appears to be due to interdigitation across the suture, rather than a true process. In *Elseya latisternum*, the continuation of the fronto-parietal suture lateral to the posterior process of the frontal is straight, and perpendicular to the axis of the skull, whereas in *Birlimarr gaffneyi* it has an anterolateral vector. The result in both cases is that the fronto-orbital is short. In contrast, in *Emydura* the fronto-parietal sutures are co-linear, perpendicular to the axis, and the fronto-orbital suture is long. *Pseudemydura* has a complex fronto-parietal suture: a medial posterior frontal process is absent, and the fronto-orbital suture is long, but shows complexity not found in other chelids. The *Pseudemydura* morphology is here considered an autapomorphy related to secondary re-roofing of the temporal fossa. No other chelids figured by Gaffney (1977) have a posterior frontal process, nor is it present in pelomedusids figured by Gaffney (1979b: *Pelomedusa subrufa*, ~fig. 130; *Pelusios niger*, ~fig. 132; *Bothremys cooki*, ~fig 125; *Schweboemys antiqua*, ~fig. 136; *Erymnochelys madagascariensis*, ~fig. 129; *Peltocephalus dumeriliana*, ~fig 131; *Podocnemis expansa*, ~fig. 134) or in *Araripemys barretoi* (Meylan 1996: fig. 4). In SMF 4922 (Gaffney and Meylan 1991), it is the frontals which are partly separated by short, broad anterior processes of the parietal. We therefore hypothesise that the absence of a

posteromedial frontal process is the primitive state for chelids. (Somewhat similar structures in the cryptodirans *Malaclemys terrapin*, Gaffney 1979b: fig. 244; *Clemmys insculpta* ~fig. 231; and *Chrysemys concinna*, ~fig. 229, must have evolved independently).

10. Anterior basiphenoid process stops short of the level of the lateral trochlear processes of the pterygoids. In *Pseudemydura, Emydura, Rheodytes* and *Birlimarr gaffneyi* the anterior basiphenoid process fails to reach the level of the lateral trochlear processes of the pterygoid, whereas it clearly does reach or projects beyond in all other chelids. Amongst pelomedusids figured by Gaffney (1979), the anterior basisphenoid process shows the elongate condition in *Pelomedusa subrufa*, ~fig. 130; *Pelusios* sp., ~fig. 34C: *Pelusios niger*, ~fig. 132; *Bothremys cooki*, ~figs 125, 126; *Schweboemys antiqua*, ~fig. 136; and *Erymnochelys madagascariensis*, ~fig. 129. The exceptions are *Peltocephalus dumeriliana* (Gaffney 1979b: fig. 131) and *Podocnemis expansa* (Gaffney 1979b: fig. 134), which at generic level comprise the un-named taxon B11 in Gaffney and Meylan (1988). Taxon B11 is shown in Gaffney and Meylan (1988: fig. 5.7) as the most derived pelomedusid clade, and therefore probably not representative of the ancestral state for the two families. *Araripemys barretoi* shows the elongate condition (Meylan 1996: fig. 4), as does SMF 4922 (Gaffney and Meylan 1991). We hypothesise that the elongate basisphenoid condition is primitive for both pelomedusids and chelids, and that the reduced state was independently derived within these families.

11. Ventral ridges of frontal bone vertical and parallel (Cann and Legler 1994: table 4, character 3). Amongst short-necked chelids, the ventral ridges of the frontals are either parallel and vertical (*Elseya dentata, Rheodytes, Elusor, Emydura, Pseudemydura*, and *Birlimarr gaffneyi*) or turned sharply inwards (*Pseudemydura* and *Elseya latisternum*). Amongst pelomedusids, where mentioned or figured, the ridges appear to be weakly developed (*Araripemys barretoi* - Meylan 1996: 23; *Pelusios* sp. - Gaffney 1979b: fig. 4; *Taphrosphys sulcatus* - Gaffney 1979b: fig. 138). It therefore seems possible that well-developed ridges are a shared derived character of chelids, but whether the two different expressions of the character evolved independently, or one gave rise to the other, is unclear. Cann and Legler (1994) nominated *Chelodina* as their outgroup - in *Chelodina rugosa* the ridges are turned sharply inwards – implying that this is the primitive state for chelids. A slight constriction is also evident in *Pelusios* sp. (Gaffney 1997: fig. 4), and thus we accept the view that this represents the primitive state for chelids.

12. Axillary and inguinal buttresses of approximately equal size (Cann and Legler 1994: Table 4, character 11). In *Elusor* and *Rheodytes* the inguinal and axillary butresses contribute about equally to the bridge, whereas in all other short-necked chelids, including *Birlimarr gaffneyi*, the axillary contributes proportionally more. Most pelomedusids retain mesoplastra, complicating the interpretation of the primitive state for chelids. In *Araripemys barretoi*, which is unusual amongst pelomedusids in lacking mesoplastra and has other peculiarities of the shell, the inguinal buttress is larger than the axillary (Meylan 1996: fig. 2). In the more generalised early pelomedusid, SMF 4922, a projection of the hyo-hypoplastral suture through the mesoplastron would suggest that the axillary buttress would come to form more of the bridge than the inguinal, were the evolutionary trajectory simply one of the hyo- and hypoplastra replacing the mesoplastra in this manner. This is taken here as reflective of the primitive condition in chelids.

13. Quadrate parietal contact (Gaffney 1977: identified as an autapomorphy of a monospecific Pseudemydurinae). Quad-

rate-parietal contact is a derived feature of the extant Western Swamp Tortoise, *Pseudemydura umbrina*. In the Miocene fossil skull from the Carl Creek Limestone of Queensland, QM F31305 (Fig. 31) (White 1997), the more complete right hand side of the skull is damaged in the critical area, but unless the missing portion of the squamosal-parietal suture somehow followed a significantly different course from that of *Pseudemydura*, it would appear that the quadrate and parietal did make contact. This feature is attributed by Gaffney (1977) to a secondary re-roofing of the temporal fossa.

14. Supraoccipital laterally expanded (Gaffney 1977: identified as an autapomorphy of a monospecific Pseudemydurinae). In *Pseudemydura umbrina* the supraoccipital of the skull roof is laterally expanded compared to the typical chelid (and the pelomedusid outgroup) condition, to the extent that the supraoccipital usually contacts the squamosal laterally. thereby excluding the parietal from the posterior skull margin (Fig. 31). In QM F31305, the supraoccipital is less in its extent than in *Pseudemydura umbrina*, such that the parietal remains interposed between it and the squamosal. Parietal interposition between the supraoccipital and squamosal is a feature of Ringtail Site, Carl Creek Limestone *Pseudemydura* sp., QM F17415, described by Gaffney *et al.* (1989: fig. 1) (Fig. 31). Although not as expanded as in *Pseudemydura*, the supraoccipital of QM F31305 is significantly expanded compared to the plesiomorphic condition.

15. Postorbital posteriorly and ventrolaterally expanded. Gaffney (1977) observed that the postorbital is large in *Pseudemydura*, expanded ventrolaterally compared to its small dorsal expression in all other chelids and the pelomedusid outgroup, and therefore nominated it an autapomorphy of the Pseudemydurinae. Loss of the quadratojugal is a shared derived character of chelids apparently related to extreme lateral cheek emargination. Pelomedusids retain a quadratojugal, even in species showing quite a significant degree of lateral cheek emargination. Pelomedusids figured by Gaffney (1979b) show no great consistency in the size and shape of the postorbital, ranging from proportionally very small in *Podocnemis expansa* (Gaffney1979b: fig. 134); to quite substantial in *Schweboemys antiqua* (Gaffney1979b: fig. 136). In *Araripemys barretoi* (Meylan 1996: fig. 4A) it is of intermediate size within the range expressed by *Podocnemis* and *Schweboemys*, though long and narrow compared to most pelomedusids, including the more generalised early pelomedusid SMF 4922 (Gaffney and Meylan 1991). Meylan (1996) indicates that a long postorbital is primitive for pleurodires, and scores Chelidae as fundamentally exhibiting the primitive state, with pelomedusids exhibiting derived conditions in which the postorbital is shortened, the parietal and jugal variously making or not making contact. Gaffney (1977) argues that a ventrolaterally expanded postorbital is related to the secondary re-roofing of the temporal fossa in *Pseudemydura*. The postorbital of QM F31305 is very similar in size and extent to *Pseudemydura* (Fig. 31).

While the postorbital of *Birlimarr* is not as large as that of *Pseudemydura* and QM F31305, it is proportionally somewhat larger than in all other short-necked chelids. It is similar to *Pseudemydura* and QM F31305 in terms of the relative proportion of its contribution to the orbital margin, though its posterior development is notably less, but ventral development perhaps only slightly less. There are several ways of interpreting this character amongst Australian short-necked chelids. One possibility is that a relatively large postorbital (or at least relatively large contribution to the orbital margin) represents a synapomorphy of *Pseudemydura, Birlimarr* and QM F31305. Alternatively, the large contribution to the orbital margin in *Birlimarr* evolved independently of *Pseudemydura* and QM F31305, which is our preferred hypothesis in the absence of other possible derived states shared only by these taxa. We therefore adopt a slightly modified form of Gaffney's (1977) definition of the derived state, treating *Birlimarr* as exhibiting the primitive state in terms of overall postorbital size.

16. Anterior extension of squamosal (Gaffney 1977: identified as an autapomorphy of a monospecific Pseudemydurinae.) In *Pseudemydura*, the squamosal is expanded anteriorly to roof the posterolateral portion of the temporal fossa. It is developed anteriorly to a similar extent in QM F31305.

Discussion and conclusions. A generic-level analysis of apparently derived morphological characters of short-necked chelids using Hennig86 (Farris 1988) produces two equally short trees (Fig. 32). *Birlimarr* is resolved as one of the more derived genera, the plesiomorphic sister taxon only to *Emydura* + *Elseya dentata* GG.

Of seven characters identified by Gaffney (1977) as autapomorphies of *Pseudemydura*, the five which can be assessed for QM F31305 are shared. QM F31305 is thus resolved in this analysis to be a member of Gaffney's (1977) previously monospecific Pseudemydurinae. White (1977) details the morphological differences between *Pseudemydura umbrina* and QM F31305, drawing attention to osteological details suggesting an unusual distribution of the musculature between cranium and lower jaw. He concluded that QM F13305 cannot be referred to any known infraorder or genus. However, the nature of the jaw articulation is fundamentally pleurodirous, in that a processus trochlearis pterygoideus is present. Furthermore, the specimen shares at least two shared derived characters diagnostic of the Chelidae (1 and 2 of this work), but the sole identified synapomorphy of Chelinae (4 of this work) cannot be assessed. QM F31305 appears be too specialised to have given rise to *Pseudemydura umbrina* and Carl Creek Limestone *Pseudemydura* sp., but the present indications are that these forms are closer to each other than each is to something else.

The only difference between the two hypotheses of relationships advanced here (Fig. 32) is whether the Pseudemydurinae (*Pseudemydura* + QM F31305) or the *Elseya latisternum* generic group is the plesiomorphic sister-taxon to all other Australasian short-necked chelids. It is conceivable that the Pseudemydurinae evolved from an *Elseya latisternum*-like form early in chelid evolution (possibly in the Cretaceous), but in the absence of adequate comparative fossil material until the Miocene, the possible morphology of an ancestral chelid can only be inferred. The alternative hypotheses are seen here simply as artifactual of limited morphological data, rather than a basis for a particular perspective on early chelid evolution.

Comparison of the phylogenies of the short-necked chelids based on morphological data (Figs 2, 20, 32) and molecular data (Figs 3, 4) reveals certain similarities. Both lines of evidence indicate that *Elseya* is paraphyletic, and that *Pseudemydura, Elusor* and *Rheodytes* are, in that order, progressively less plesiomorphic members of the group. The geochronological (mid Miocene) age of *Birlimarr*, and its phylogenetic position relative to *Emydura*, also supports the idea from molecular data that *Emydura* evolved relatively more recently than other genera (Georges and Adams 1992, 1996).

While *Elseya* appears to be paraphyletic, it is not yet firmly established which species form monophyletic groups (compare Figs 3, 4 and 20). Some better understanding is required of the extent to which *Elseya latisternum* is generically characteristic of its group, as it appears variously as representative of a plesiomorphic generic group (Figs 20 and 32 A, B), as representative of a more derived generic group (Fig. 3), and as one of the two most highly derived chelids (Fig. 4B). A need for comprehensive comparative osteologies of all living species is evident, both to test phylogenies founded in biochemistry, and to complement stratigraphic evidence of chelid evolution.

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